University of Alberta

Identifying Potential Critical Habitat for Western Burrowing Owls (*Athene cunicularia hypugaea*) in the Canadian Prairies

by

April F. Joy Manalo Stevens

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ABSTRACT

Critical habitat definitions for endangered species require quantitative knowledge of a species' use of its environment. I compared two species distribution modelling techniques for the Burrowing Owl (*Athene cunicularia*) in Prairie Canada. My comparison revealed that Ecological Niche Factor Analysis (ENFA) models can provide robust ecological indications of habitat suitability, while a carefully designed logistic regression Resource Selection Function (RSF) model can provide better spatially explicit predictions. I created six RSF habitat selection models, and determined that home-range use was best predicted by large-scale, abiotic factors (soil and climate), rather than grassland fragmentation or land-use type. Furthermore, nest survival and fledgling production did not vary with respect to this presence-based home-range selection. My research indicates that the unique soil and climate conditions that are associated with breeding Burrowing Owls home-range selection are important factors for narrowing the delineation of potential critical habitat for this species.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 CRITICAL HABITAT IN CANADA

As of September 2007, 539 species were listed as being 'at risk' of extinction in Canada (COSEWIC 2007). Declines of most endangered and threatened species in Canada are thought to be associated with habitat loss and fragmentation; as such, the Species-at-Risk Act regulates habitat protection and management for all listed species. The Act defines habitat[1] as species-specific, with critical habitat[2] defined as 'the habitat that is necessary for the persistence and recovery of a listed wildlife species'. This management definition is contingent upon the identification of critical habitat within the recovery strategy[3] or action plans[4] for each individual species. In this context, legal designation of areas identified as critical habitat does not exist until an approved recovery strategy or action plan delineates the bounds of the critical habitat. To date (August 2008), 67 recovery strategies have been finalized, with 160 delayed.

In Canada, the definition of critical habitat is legalized by the 'Responsible Minister' – either the Minister of the Environment, Fisheries and Oceans, or Parks Canada. However, recovery teams have the responsibility of providing advice and making recommendations for critical habitat designations. Recovery teams typically consist of Species-at-Risk biologists and managers (both federal and provincial), species experts, associated non-governmental organizations, land managers, industry, First Nations, and public representatives, as appropriate. Along with any relevant published research, recovery team members are the main source of scientific and expert advice for defining critical habitat. Discussions among recovery team members on how to define

critical habitat have mainly focused on how to fill ecological data-gaps and assess socio-economic factors that limit the ability of government agencies to manage habitat resources. Less attention has been paid to the methods of analyzing habitat relationships and identifying approaches to modelling such data. Most recovery teams have described the biophysical attributes required by a species, typically based on qualitative literature reviews. The lack of a cohesive, quantitative framework for defining the spatial bounds of critical habitat remains a challenge for most recovery teams; however, the variation in species – from molluscs to plants to large mammals – and their unique ecological needs, makes it difficult to prescribe one all-inclusive framework. Effective support and implementation of critical habitat designations requires: 1) quantitative methods capable of creating spatially explicit predictions of critical habitat; 2) recognition of spatial and temporal scale when making decisions about what habitat is critical; and 3) ecologically based criteria of habitat needs that are linked to the main demographic factors that limit population growth in individual species. The goal of my thesis is to address these issues and to identify potential critical habitat for the endangered Western Burrowing Owl (*Athene cunicularia hypugaea*; herein, Burrowing Owl) in the Canadian prairies.

1.2 SPECIES DISTRIBUTION MODELS

Species Distribution Models (SDMs) are useful tools for evaluating critical habitat requirements for endangered species, as they quantify the relationship between species and their environment using empirical data (Guisan and Zimmerman, 2000; Johnson and Gillingham, 2005). However, note that species distribution is only *one* component of critical habitat, describing where species are currently found or where they have the potential to be found (see discussion below on habitat quality). Most SDM

applications are correlative in nature, meaning that the mechanisms that make one habitat type better than another are not explicitly tested. Instead, ecologists assume that, by identifying environmental features with which species occurrence or abundance are correlated, necessary resources such as food, shelter, and reproduction sites will be present (Corsi et al., 2000; Guisan and Zimmermann, 2000). The choice of an appropriate modelling technique can be difficult, because each approach may be unique in the underlying ecological questions and hypotheses it can address (Guisan and Zimmerman, 2000).

Many different SDM techniques have been developed; for example, Ecological Niche Factor Analysis (ENFA; Hirzel et al. 2002), Mahalanobis distance (e.g., Clark et al. 1993; Rotenberry et al., 2006), and resource selection functions (RSFs; Manly et al., 2002). Each technique has various limitations and assumptions that can affect what is predicted as a species' distribution and, therefore, the spatial bounds of what is deemed potential critical habitat. For example, Johnson and Gillingham (2005) evaluated four SDMs – a qualitative Habitat Suitability Index (HSI), a quantitative RSF, a Mahalanobis distance model, and an ecological niche model – for radio-collared woodland caribou (*Rangifer tarandus caribou*). They developed models for three sets of independent variables, using all four approaches, and then evaluated these models with a temporally independent set of locations. They also compared the similarities and differences of the four species distribution maps that were produced. Their evaluation showed that each of the quantitative SDMs were better predictors than the qualitative HSI; however, the spatial distribution of the habitats was quite variable among the quantitative SDM models. This has obvious implications for the delineation of critical habitats. Careful

consideration of the exact objectives of a study, the ecology of the species, and the availability of species location and environmental data is needed when choosing a particular modelling framework.

1.3 ISSUES OF SCALE AND ORDERS OF SELECTION

Which analytical technique is best to use when modelling critical habitat is in part an issue of scale. Recent advances in landscape ecology have clearly demonstrated the importance of spatial and temporal dynamics of species-environment relationships at various scales (Corsi et al., 2000; Garshelis, 2000; Boyce et al., 2002; Guisan and Thuiller, 2005). Relationships that appear to be important within a local study site are not necessarily applicable on a regional level. For instance, Wiens et al. (1987) found that habitat use and selection patterns by several shrub steppe bird species in North America varied depending on the spatial scale analysed. Johnson (1980) emphasized that conclusions drawn from any use-versus-availability study depend on the researchers' definition of what resources are available to the animal in question. As such, Johnson (1980) introduced the now well-known hierarchical ordering of selection processes: first-order selection is the geographic range of the species, second-order is the home-range within the geographic range, third-order is the usage of various components of habitat within the home-range, and fourth-order is the attainment of resources within those home-range habitat components. Temporal processes can be thought of as a similar metric, where resources are defined by their availability during a specified range of time (e.g., breeding season vs. non-breeding season resources; pre- vs. post- human developments on a landscape). Critical habitat is inherently linked to the hierarchical

nature of these properties, and understanding these relationships at each scale of selection is vital to the definition of critical habitat for a species.

Most SDMs are generated at the first-order geographic range; whereas, the most common use-versus-availability models define habitat selection (the disproportionate use of resources; Manly et al., 2002) at the third-order scale. As well, management plans and study designs are typically drawn up for localized areas, such as national or provincial parks. Therefore, recovery teams that use literature reviews to define critical habitat are mostly confined in their definition to third-order selection. Geographic range is species-specific, varying from one small pond to an entire continent. However, most habitat models for species that range over large areas do not account for regional variation that might be driven by large-scale processes, such as climate, soils, or other macro-ecological processes (factors more likely to be observed at second-order selection). These regional processes could dictate how species are distributed and using habitat on finer scales of selection, if used habitat components differ from one region to another. To link all of these processes together into a concise definition of critical habitat, recovery teams need to understand how species' habitat use can change depending on the order of selection.

1.4 HABITAT QUALITY

As mentioned above, species distribution is only one component of what defines critical habitat. Recovery teams can adopt the terms "suitable" and "essential" to narrow the extent of critical habitat. I consider suitable habitat to describe where the species' occurs (or has occurred), or its distribution, while essential habitat is that which is necessary for populations to persist and grow. These two concepts can be measured independently; however, they must be considered simultaneously to define critical

habitat. For example, population growth cannot happen without species presence, and species presence fades without population growth and replacement. Another term frequently used in the scientific literature is that of habitat quality, defined as "the *per capita* contribution to population growth expected from a given habitat" (Johnson, 2007). High-quality habitat can therefore be thought of as the most essential component of critical habitat. Optimally, critical habitat definitions encompass high-quality areas with a high number of animals, which allows for more rapid population growth, and faster recovery of a species.

Density, however, is not always an indicator of habitat quality (Van Horne, 1983). Van Horne (1983) points out that population size may have been determined at a time or place other than when it was measured or species' hierarchy dynamics force lower-ranked individuals to crowd into sub-prime areas. Possibly the most relevant issue for species-at-risk is the case where anthropogenic disturbances alter a species' ability to recognize and select high-quality habitat (Bock and Jones, 2004). To disentangle potentially 'false' indicators of high-quality habitats (e.g., density of individuals) from actual high-quality habitat that needs to be protected, recovery teams need to relate resource use and availability to population persistence and growth.

1.5 STUDY SPECIES AND AREA

Burrowing Owls are unique in North America as fossorial owls, nesting in abandoned, underground burrows, most commonly created by prairie dogs, ground squirrels and badgers (Haug et al., 1993; Poulin et al., 2005). They are small owls (~160g; Wellicome, 2005), with some evidence of sexual dimorphism as females are heavier, and males are slightly larger in some linear measurements (Plumpton and Lutz,

1994). Plumage differences have also been described, as females are typically found to be slightly darker than males during the breeding season (Haug et al., 1993). They are short-lived, as no banded owls were found to be over six-years old during a long-term study in Saskatchewan (D. Todd, R. Poulin, and T. Wellicome, unpubl. data). The Canadian population is migratory, arriving during the summer season to breed (~ April to September; Haug et al. 1993). The natural ecology and life-history traits of the Burrowing Owl during this time are well studied. Males usually arrive first on breeding grounds, establishing territories and preparing potential nesting burrows, and begin courtship when females arrive (Haug et al., 1993). Burrowing Owls are monogamous during the breeding season; however, pair bonds are not permanent (Haug et al., 1993). Typically only one brood is attempted per season, with egg laying beginning soon after pair formation in May (Haug et al., 1993). Approximately 1 egg is laid every 1.5 days with typical clutch sizes ranging from 6-12 eggs (Wellicome, 2005). The incubation period (first egg to first hatch) lasts approximately 30 days, with incubation by the females only (Haug et al., 1993). After hatching, the female does all brooding until the young are capable of autothermoregulation (Haug et al., 1993). Male owls hunt and provide food during incubation and brooding, until the young are less dependent, approximately 2 weeks post-hatch, at which point the female also hunts (Haug et al., 1993). Juveniles are mobile and can be seen at the burrow entrance around 14 days (Haug et al., 1993). They often engage in temporary dispersal movements from the nest burrow to satellite burrows prior to permanent departure from the nest (Davies and Restani, 2006; T. Wellicome, pers. comm.), which occurs approximately 53 days post-hatch (Todd et al., 2007).

Largely because of a declining population over the past several decades, the Burrowing Owl is classified as an endangered species in Canada (COSEWIC 2006). Historically, this owl was common across the four western provinces that encompass the potential range of the species in Canada; currently, Alberta and Saskatchewan are the only provinces with naturally occurring breeding populations. In British Columbia, the species was considered extirpated in 1978, and the current breeding population exists because of annual reintroductions (Wellicome and Haug, 1995; Mitchell 2008). In Manitoba, the last confirmed nesting pair was seen in 1999 (K. DeSmet, unpubl. data), although unconfirmed sightings of a few owls have been reported each year. Throughout North America, modern agricultural practices and associated increases in human activities have resulted in widespread loss and fragmentation of grassland, which are commonly presumed to be the ultimate factors for the Burrowing Owl population decline (Wellicome and Haug, 1995; CEC 2005).

In the Canadian prairies, the current breeding range of the Burrowing Owl covers over 18 million ha in southeastern Alberta and southern Saskatchewan, from the Canada-U.S. border (49th parallel) to 52°50′N latitude and 113°0′W and 103°30′W longitude (see Figure 1.1). This area is located within the mixed prairie of the Grassland eco-region, with a diverse plant community dominated by medium-height grasses (e.g., needle and thread, *Stipa comata*), short grasses (e.g., blue grama, *Bouteloua gracilis*), and sedges (Trottier, 1992). Land use is dominated by mixed agricultural practices (51%), ranching activities on native and non-native grassland (40%), and oil and gas activity (roads, wells, pipelines, compressors). This area holds the majority of known breeding Burrowing Owls in Canada, and the current naturally occurring population.

Qualitative descriptions summarize Burrowing Owl habitat as short grass, open terrain on relatively flat, treeless plains, associated with fossorial mammals (Wedgwood, 1978; Haug et al., 1993). Past research on Burrowing Owl habitat has focused mainly on these qualitative site descriptions (e.g., Coulombe, 1971; Wedgwood, 1978) and third- and fourth-order processes (Johnson, 1980) that operate on small-scale environmental relationships (e.g., Green and Anthony, 1989; Poulin et al., 2005). Tall vegetation and permanent cover within the species' foraging home-range are assumed to be important for providing an adequate prey supply, which is required in addition to a suitable nest burrow in an open area immediately surrounded by short vegetation (Wellicome and Haug, 1995).

1.6 THESIS OVERVIEW

In this thesis, I examine some of the technical and ecological aspects related to the definition of critical habitat for Species-At-Risk in Canada. Specifically, I create several models describing species-environment relationships of the endangered Burrowing Owl to identify suitable and essential breeding areas in the Canadian Prairie region. The historical and current geographic range of the Burrowing Owl (first-order selection) is well known and defined in this area (COSEWIC 2006). Also, regional studies within this range, describing nest-burrow and foraging-site selection (third-order habitat selection), have been conducted or are ongoing (see thesis work and published literature from E. Haug, R. Poulin, D. Shyry, R. Sissons, and T. Wellicome). However, within this region, there is a lack of information on home-range habitat selection (second-order selection). Therefore, I will attempt to fill this knowledge gap and explore Burrowing Owl home-

range habitat selection and examine how it relates to high-quality habitat at the same spatial scale.

In Chapter 2, I examine the predictive ability and model performance of two different SDM techniques. Based on this analysis, I choose one technique to continue my analysis of home-range habitat selection. In Chapter 3, I investigate large-scale environmental predictors of home-range selection, and determine the effects of these large-scale predictors on suitable vegetation cues. The results of this analysis provide a definition of suitable, high-use areas within the Burrowing Owl's prairie range. In Chapter 4, I examine potential links between these high-use areas and high reproductive success, in terms of nest survival and fledgling production. In Chapter 5, I summarize my results, discuss limitations of my study and future research needs, and make recommendations for modelling and defining critical habitat for Burrowing Owls and other Species-At-Risk in Canada.

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1 "Habitat" means (a) in respect of aquatic species, spawning grounds and nursery, rearing, food supply, migration and any other areas on which aquatic species depend directly or indirectly in order to carry out their life processes, or areas where aquatic species formerly occurred and have the potential to be reintroduced; and (b) in respect of other wildlife species, the area or type of site where an individual or wildlife species naturally occurs or depends on directly or indirectly in order to carry out its life processes or formerly occurred and has the potential to be reintroduced.

2 "Critical habitat" means the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species.

3 "Recovery strategy" means a recovery strategy included in the public registry under subsection 43(2), and includes any amendment to it included in the public registry under section 45.

4 "Action plan" means an action plan included in the public registry under subsection 50(3) and includes any amendment to it included in the public registry under section 52.

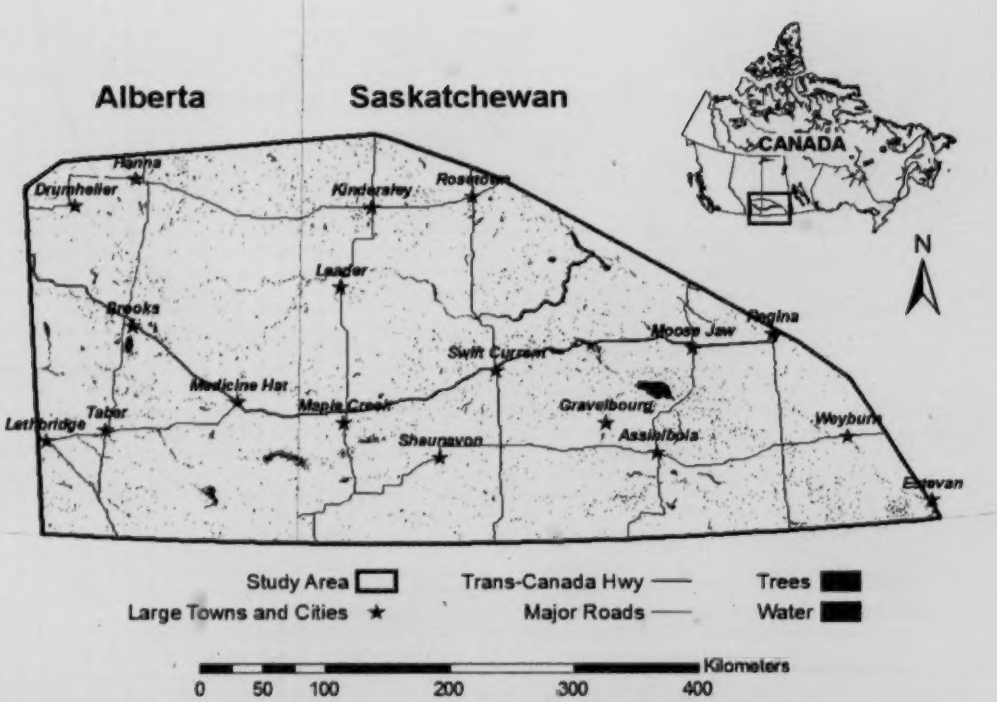

Figure 1.1. The study area located within the mixed grassland eco-region of south-eastern Alberta and southern Saskatchewan. Dominant land-uses include mixed agricultural practices (51%), ranching activities on native and non-native grassland (40%), and oil and gas activity (roads, wells, pipelines, compressors). This area approximates the current geographic range of Burrowing Owls within the Canadian Prairie region, encompassed by the towns of Lethbridge (112.81407, 49.69773), Drumheller (112.63263, 51.42054), Estevan (102.99084, 49.139679), and Rosetown (107.99069, 51.54930; all locations given as longitude and latitude decimal degrees, respectively).

CHAPTER 2. COMPARING ECOLOGICAL NICHE FACTOR ANALYSIS AND LOGISTIC REGRESSION RESOURCE SELECTION FUNCTIONS USING AN ENDANGERED SPECIES

2.1 INTRODUCTION

The integration of Species Distribution Models (SDMs) with Geographical Information Systems provides ecologists and wildlife managers with a powerful tool, especially for large spatial scales. Typically, conservation biologists use SDMs to help determine suitable habitat sites and make predictions about the size of populations that can be supported by those habitats (Boyce and McDonald, 1999; Hirzel et al., 2004; Thatcher et al., 2006). This same approach can be used when modelling endangered species, though these species present some unique challenges (Engler et al., 2004; Norris 2004). With species that have declined, location data can be scarce and is often not associated with known absence points (commonly referred to as 'presence-only' data). Furthermore, ecological knowledge of endangered species under optimal conditions is often impossible. Most SDMs work best when assuming that the species is in equilibrium with its environment (Guisan and Thuiller, 2005), which is not the case for declining populations.

A fundamental difficulty for endangered species biologists is choosing the appropriate statistical modelling technique given the above constraints. The availability and number of SDMs has increased over the past few decades, which has prompted several studies that document species-environment relationships under varying circumstances. Most of these studies apply a single technique to help define habitat

requirements for a single species (e.g., Hirzel et al., 2004; Johnson et al., 2004; Browning et al., 2005; Richardson et al., 2005). However, the extensive array of choices causes much confusion, and there is a need to examine the performance of each technique in terms of prediction accuracy. Several recent studies have attempted to clarify some of the uncertainties related to choosing a technique (e.g., Brotons et al., 2004; Segurado and Araujo, 2004; Johnson and Gillingham, 2005; Olivier and Wotherspoon, 2006), however, the general consensus from these studies is that one universally applicable technique does not exist. As well, these studies have not directly compared the ecological interpretability of model results – specifically, examining if the model attributes concur with what is known about the species' natural history and ecology. The implications of using a model that predicts well without examining the ecological reality of the model can be detrimental. In the case of endangered species, managers need to justify the ecological consequences of their policies and decisions and, if variables "do not make sense", credibility can be lost. Biologists must carefully consider the available species data and known ecological characteristics of the species before choosing a modelling technique.

Pearce and Boyce (2006) presented a review of modelling species distribution with presence-only data. One approach is to contrast the distribution of presence sites with the available environment. Two common and easy-to-use techniques based on this approach are the Ecological Niche Factor Analysis (ENFA, Hirzel et al., 2002) and resource selection functions (Manly et al. 2002). ENFA compares the environmental conditions of presence locations to the available environmental conditions across the entire study area. The ENFA employs a two-step approach: first is a factor analysis to summarize environmental variables into fewer, uncorrelated ecological factors; and

second, a habitat suitability model is computed using the most important factors from the factor analysis as predictor variables (Hirzel et al., 2002). In comparison, a resource selection function is any mathematical function that provides a value for a resource unit that is proportional to its probability of use by an organism. The logistic regression resource selection function use-versus-availability technique (herein, RSF) contrasts a sample of species presence locations with a random sample of available locations, estimating relative likelihoods of use with an exponential model (Manly et al., 2002).

Regardless of technique, SDMs can best define critical habitat for endangered species when the models are based on reliable, scientific research that has established the variables that influence species–habitat relationships. An *a priori* selection of variables is hard to justify biologically without sufficient background knowledge – typical of endangered species – so one solution is to include all potentially relevant variables. However, including a greater number of variables can create models which are ineffective for ecological interpretation and also introduce statistical problems such as collinearity and variable redundancy (Hirzel et al., 2002). Hirzel et al. (2001) suggest that an ENFA is ideal when ecological knowledge is insufficient to develop *a priori* candidate models and an evaluation of many potential variables is required. In contrast, an RSF is inherently linked to a solid knowledge of the species-environment relationship (Hosmer and Lemeshow, 2000; Manly et al., 2002), and pre-screening to reduce the number of correlated predictor variables is a general practice.

To date, no empirical studies have directly compared RSFs to ENFA models. However, studies have been published that compare ENFA to logistic regression Generalized Linear Models (comparing presence vs. absence or 'pseudo'-absence),

focusing solely on predictive capabilities under various scenarios. Performance under varying species abundance (Hirzel et al., 2001), marginality and prevalence (Brotons et al., 2004), distribution (Segurado and Araujo, 2004), and the quality of species location data (Engler et al., 2004) have all been examined. Most studies have concluded that the two methods provide similar results but that Generalized Linear Models have greater predictive accuracy under optimal data quality and species conditions (common and in equilibrium with the environment; Hirzel et al., 2001).

The objective of this study is to analyze the predictive ability and ecological interpretations of two SDM techniques, the ENFA and RSF. I also examined how model performance is affected by including a greater number of covariates as well as the associated issue of collinearity. Collinearity occurs when predictor variables show a strong degree of correlation, typically indicated by significant Pearson or Spearman pair-wise correlation statistics (approximately >0.7). Bonate (1999) found that collinearity can inflate the standard errors of parameter estimates in regression analysis. This could cause significant relationships to go undetected because the confidence interval around the parameter coefficients will increase to include zero, indicating no effect. As well, collinearity may bias the actual value of the parameter estimates (Bonate, 1999), resulting in false species-environment relationships. Manel et al. (1999) alluded to the sensitivity of logistic regression to collinearity in predictor variables while ENFA approaches are considered to be robust to collinearity issues; however, a formal investigation of model performance has not been conducted.

In this study, I used the same base set of environmental predictor variables with both the ENFA and RSF, under high to low levels of collinearity, to produce habitat

suitability models for the endangered Burrowing Owl in the Canadian prairies. I measured predictive performance across all models using temporally independent location data. I then examined patterns in the variables to assess the ecological interpretations of each technique. The Burrowing Owl presents an interesting case study, because knowledge of the habitat requirements of the species at large spatial scales is limited, and *a priori* decisions in variable selection can be subjective.

2.2 METHODS

2.2.1 Species Location Data

For Burrowing Owls, presence-only data is the only available data because no large-scale systematic surveys exist for this species. I developed all SDMs with location data provided by two provincial government databases: the Alberta Fish and Wildlife Management Information System and the Saskatchewan Conservation Data Centre. These data represent presence-only locations where observers detected Burrowing Owls (e.g., visual observation or Burrowing Owl food pellets located near burrows). I constrained these data to the extent of the study area (see Chapter 1 for a description), from ~1987–2004, which covers almost all of the current range of the owls.

The Canadian Wildlife Service (CWS) provided an additional set of location data that were collected during a large-scale Burrowing Owl monitoring project undertaken by T. Wellicome. From 2003–2006, this project located Burrowing Owl nests and other incidental presence-only detections by re-surveying known previous nesting sites and searching the surrounding landscape. Additional locations were obtained through cooperation with other biologists, land owners and managers with knowledge of breeding Burrowing Owl locations. To evaluate the models built with the provincial databases, I

used a subset of the CWS data recorded from 2005-2006. This subset provided a temporally independent data set for model evaluation.

2.2.2 Environmental Data

Qualitative descriptions summarize Burrowing Owl habitat as short grass, open terrain, on relatively flat, treeless plains, associated with fossorial mammals (Wedgwood, 1978; Haug et al., 1993). I selected 19 environmental predictor variables corresponding to this description and the availability of spatial data layers (Table 2.1). I created a raster layer for each variable with a 30-m pixel resolution. Haug and Oliphant (1990) found that the maximum home-range size of Burrowing Owls was approximately 4.8-km^2, which is equivalent to a circle with a 1.2-km radius. For every variable, each 30-m pixel in my maps summarizes the information within the neighbouring 1.2-km radius landscape. I derived proportional, distance, and fragmentation land-use variables from the Prairie Farm Rehabilitation Association dataset (land cover grid), elevation and slope variables from a Digital Elevation Model provided by Parks Canada (Swift Fox Recovery Team)[1], and road metric variables from the National Road Network Canada database. To provide a consistent comparison, I included only the linear forms of each variable in the modelling approaches compared in this chapter, though non-linear relationships between selection and habitat covariates are common (see Chapter 3).

To assess collinearity within the dataset, I calculated the correlation matrix among all variables using BIOMAPPER 3.2 software (Hirzel et al., 2006; Table 2.2). The majority of the variables were uncorrelated; however, I found various levels of collinearity among seven of the variables. I divided the levels of collinearity into four

categories: high (>0.90), strong (0.75-0.90), weak (0.50-0.75), and low (<0.50). I used these categories as the basis for building each SDM under high to low collinearity levels.

2.2.3 Statistical Modelling

I explored two common SDM presence-only techniques: the ENFA and RSF. Both techniques produce mathematical functions that can provide relative ranks of habitat suitability for comparison purposes.

Ecological Niche Factor Analysis (ENFA)

I used the BIOMAPPER 3.2 software (Hirzel et al., 2006) to calculate ENFA models describing Burrowing Owl habitat suitability, following the methods outlined in Hirzel et al. (2002). I used the 'box-cox' transformation (Sokal and Rohlf, 1981) within BIOMAPPER to normalize any non-normal data before model building, and included these transformed variables in both the ENFA and RSF modelling techniques. BIOMAPPER software performs predictive habitat modelling in two steps: first, the ENFA summarizes the environmental predictor variables into principal component factors that can be used to describe habitat suitability given the available data; and second, those factors that explain the most variance are used as predictors to create a predictive habitat suitability model and map.

Hutchinson's (1957) concept of the ecological niche forms the basis for the ENFA, where the species' niche is a subset of the overall available environment. Hirzel et al. (2002) characterize this niche using an ordination approach, similar to a Principal Components Analysis, to organize data in a multivariate environmental space. ENFA reduces the number of variables into fewer, uncorrelated, ecologically meaningful factors by comparing the species distribution (described by the presence-only locations) on X

environmental variables to the global (overall) distribution of the same *X* variables. The calculations used within the ENFA assume that species distribution is non-random within the multivariate environmental space (Hirzel et al., 2002). For example, a species with a preference for low elevation is expected to occur in areas with lower elevation, as compared to the global average elevation within the study area.

ENFA quantifies the species' niche axes in terms of marginality and specialization factors (Hirzel et al., 2002). The marginality factor, extracted first, indicates the species niche position – how far it is from average conditions in the study area. It ranges from 0-1, and describes the ecological distance between the species mean value (m_S) on *X* variable(s) and the mean of the available environment (or 'global' mean, m_G) on *X* variable(s). It is calculated by taking the absolute difference between the species mean (m_S) and global mean (m_G), and dividing by 1.96 standard deviations (σ_G) of the global distribution.

$$Marginality = | m_G - m_S | / 1.96\ \sigma_G$$

A large overall marginality value (close to 1) indicates that the species has greater restriction on its ecological requirements relative to the overall environment. The coefficient values on the marginality factor indicate the contribution of each variable to the marginality, in units of standard deviations (of the global distribution). Higher absolute coefficient values indicate a higher contribution to the marginality and a further departure from the mean available habitat, in respect to that variable. Positive values indicate selection for higher-than-mean values, and negative values indicate selection for lower-than-mean values.

The specialization factor(s) are subsequently extracted, which describe species niche breadth, sorted by decreasing amounts of explained variance. These factors quantify the specialization – or selectivity – of the species relative to the available environment. Specialization is calculated as the ratio of the standard deviation of the global distribution (σ_G) to the standard deviation of the species distribution (σ_S).

$$Specialization = \sigma_G / \sigma_S$$

Specialization is inversely related to species tolerance, where an overall specialization value exceeding 1.0 indicates some form of specialization and, therefore, less tolerance (Hirzel et al., 2002). The coefficients of the specialization factors are interpreted differently from those of the marginality factor. Higher absolute coefficient values indicate that the species is more restricted (specialized) on that variable, and coefficient signs are arbitrary.

Typically, only a few of the first factors (e.g. marginality plus 1-4 specialization factors) describe most of the variance in the dataset, and are used to calculate habitat suitability. I used a threshold value of 0.75 for cumulative variance to select the number of specialization factors included in each of the predictive habitat suitability maps. To build the habitat suitability maps within the BIOMAPPER software, I used the geometric mean algorithm, which is calculated based on the density of points in the environmental space using the geometric mean to all points (Hirzel and Arlettaz, 2003). The principle behind this method is to determine the suitability field of each species observation point within the environmental space (determined by the retained factors), such that when points are close together, the suitability field is stronger. The suitability field is calculated over the whole environmental space using the geometric mean of the distances

to all observations, for every point. Therefore, the model is calibrated in the environmental space, and then applied to the geographic space of the study area, providing a smooth set of environmental envelopes around the observation points and a good generalization of the species niche (Hirzel and Arlettaz, 2003). This algorithm makes no assumptions about the shape of the species distribution; however, the density of observations should represent the species' niche.

Logistic Regression Resource Selection Function (RSF)

A resource selection function is based primarily on habitat selection theory, where a species' disproportionate use of a resource compared to its availability is defined as selective (Manly et al., 2002). The most common form of a resource selection function is derived using logistic regression. An RSF contrasts any two of the following datasets: 1- used points (species presence locations), 2- unused points (known species absence points), or 3- available points (sampled at random without replacement from the available environment). I contrasted the presence-only ('used') points with a random sample of available points across the entire study area (n = 48726). The RSF estimates relative likelihoods using the logistic discriminant:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

where $\beta_1 \ldots \beta_n$ represent the coefficients estimated from a logistic regression model, and $w(x)$ is the relative probability of occurrence (Manly et al., 2002; Johnson et al. 2006). I performed all RSF analyses in STATA 9.0 (STATA corp., 2005).

Modelling Framework

I built ENFA and RSF models with varying numbers of predictor variables that varied in their level of collinearity (Table 2.3). At the high collinearity level, all variables

were included. At the strong level, I removed one variable at random for every pair of collinear variables above an absolute value of 0.90. For example, PG and PC are correlated at a level of -0.94; therefore I removed the PC variable from all models at the strong level, and subsequent lower levels. This procedure was continued for both the weak and low collinearity levels, with a maximum correlation of 0.75 at the weak level and 0.50 at the low collinearity level. This was done to see how each modelling technique performed with different numbers of covariates.

For each modelling technique, I performed two analyses to create two different models at each level. For the ENFA analysis, the first model, a, included all variables, after removing any collinearities according to the level of analysis. For the second model, b, I removed any variables where the absolute value of the marginality factor coefficient was < 0.05, as calculated in model a, because higher coefficient values are more important for explaining species distribution (see ENFA discussion above; Hirzel et al., 2002) and a coefficient < 0.05 may indicate redundancy. For example, at the strong level, model a (ENFA2a) included 18 variables, which was all variables minus PC, since PC and PG were collinear above the 0.90 threshold for that level. A second analysis was performed to produce model b (ENFA2b), where all variables with a marginality coefficient < 0.05, as calculated in model a, were removed. This procedure created a more parsimonious model, and simulated the 'step-wise' approach commonly used in logistic regression.

For the RSF analysis, I also analysed two models for every collinearity level. All variables were forced into the first model, a, after removing any collinearities according to the level of analysis. I then analysed a second model, b, in which I incorporated a

backwards stepwise procedure to remove any non-significant variables from model a. All of the ENFA and RSF models were then integrated into ArcGIS 9.x software (ESRI, 2004) to produce comparable habitat suitability maps.

2.2.4 Model Evaluation

To evaluate the predictive capability of each of the models, I used the temporally independent CWS dataset in conjunction with the evaluation method proposed by Johnson et al. (2006). I used quantile divisions to reclassify all of the original ENFA and RSF maps into 10 approximately equal-area bins ranked from low- to high- suitability. I used the division breakpoints to determine the midpoint value $w(x_i)$ of the original habitat suitability score for each bin, i. I calculated the area of each bin $A(x_i)$ with the total number of pixels in each bin. Using these values, I calculated a utilization value $U(x_i)$ for each of the 10 bins with the following formula (Boyce and McDonald 1999):

$$U(x_i) = w(x_i)A(x_i) \Big/ \sum_j w(x_j)\,A(x_j)$$

I overlaid the CWS dataset onto each map and tallied the number of locations within each of the 10 bins as the observed values. Expected values for each bin i were calculated by multiplying the total number of CWS evaluation points by the utilization value $U(x_i)$ of each bin i. I used linear regression statistics (constant, β_0; slope, β_1; and R^2 value) and the χ^2 goodness-of-fit to compare the expected number for each bin i to the observed number of CWS points in each bin. If a model is approximately proportional to the probability of use, the linear regression constant will be close to zero and the slope will be close to 1.0. However, the predictive power is best described by the R^2 and the χ^2 goodness-of-fit tests, which assess the fit of the model. A model that accurately predicts

observed values with the expected values will have high, positive R^2 values and a non-significant χ^2 value. R^2 represents the proportion of variance (or information) in the observed values that can be predicted from the expected values; whereas, the χ^2 statistic estimates how well the observed distribution of CWS points matches the expected distribution estimated by the statistical model. I also included the Spearman rank correlation statistic (Boyce et al., 2002) as another measure of predictive performance. I calculated the area-adjusted frequency (AAF) of the CWS points in each bin using the formula (Boyce et al., 2002; Johnson et al., 2006):

$$AAF = 0.1/A_i * U_i$$

where A_i is the proportion of available study pixels in bins i, and U_i is the proportion of CWS points within bin i. The numerator value of 0.1 was used to standardize the available pixels in each bin to produce the area-adjusted frequency. I then used these AAF values per bin in comparison to bin rank to calculate Spearman rank correlation scores for each model.

2.3 RESULTS

I developed and mapped eight ENFA and eight RSF models, using the species presence locations provided by the provincial datasets (n = 2548). Using all ENFAs, I calculated a mean species marginality of 0.38 (range 0.35 – 0.40), indicating that Burrowing Owls live in average environmental conditions. The mean specialization of 1.57 (range 1.51 – 1.65) corresponds to a tolerance level of 0.64. This indicates that the species is tolerant to environmental changes, although they do have a small amount of specialization (some 'selectivity').

Each of the models were evaluated using the temporally independent data provided by CWS (n = 359; Table 2.4). Overall, ENFA models had poor predictive ability, with linear regression statistics revealing models not proportional to the probability of use, and very weak fit between expected and observed values (e.g., $R^2 < 0.40$, and $Rs < 0.60$). The RSF models were all substantially better predictors, as indicated by the R^2 values > 0.90 and Rs values > 0.95. This discrepancy between the fit of the two techniques is illustrated in Figure 2.1, which depicts the fitted regression line for the most predictive model of each technique, ENFA4a and RSF3b. Note the dispersion of points from the regression line, as well as the slope and intercept. Chi-square goodness-of-fit tests indicated poor fit for all ENFA and RSF models (p-values < 0.05); however, all RSF models showed much better fit than any ENFA model. In general, Table 2.4 shows that decreasing the number of covariates corresponded to a slight increase in the predictive ability of the ENFA models, whereas the predictive ability of the RSF models did not change with the number of covariates included. Regardless of method, all models at the highest collinearity level were the least predictive, indicating a maximum correlation tolerance of 0.90 between variables. Figures 2.2 and 2.3 illustrate the habitat suitability maps of the least and most predictive ENFA and RSF models, respectively.

I examined variable patterns within the models to assess the ecological interpretability of each technique. The ENFA model with the most predictive ability was the full model at low collinearity, ENFA4a (Table 2.5), and therefore, I compared those model coefficients to the standardized variable coefficients included in the equivalent RSF model, RSF4a (Table 2.6). This allows for the direction and strength of coefficients

to be directly compared between methods, where a greater deviance from zero (either positive or negative) indicates a stronger association between where an animal occurs and that covariate.

In ENFA4a, the marginality coefficients indicate that Burrowing Owls are associated with flat, low areas (SL= - 0.55, EL = -0.302) and large amounts of grassland with few shrubs and trees (PG = 0.362, PS = -0.276, PT = -0.181); far from trees and shrubs (DTV = 0.385) and close to roads (DR = -0.283, RD = 0.235). The RSF4a model also indicates that Burrowing Owls are selective for flat, low areas (SL= -0.708, EL = -0.261) with large amounts of grassland with few shrubs and trees (PG = 0.538, PS = -0.222, PT = -0.096). However, this model suggests an inconsistent relationship with roads, because the association with distance to roads (DR = -0.500) increased, but the association with road density decreased (RD = 0.046) between methods. As well, the strength of the association of distance to tall vegetation (trees and shrubs, DTV) decreased in the RSF to 0.124.

Figure 2.4 illustrates the variation of coefficient values for each technique. ENFA models show less variation with relatively constant coefficient values over all models. RSF model coefficients vary greatly for a number of variables, including PH, PO, PWE and PWA, and show instability in coefficient value and sign.

2.4 DISCUSSION

This study presents a new assessment of SDM performance by comparing ENFA with RSF models, in terms of predictive ability and ecological interpretability, with changing numbers of covariates and collinearity levels. My results suggest that regardless of the variable set considered, the RSF was better at prediction than the ENFA.

However, the ENFA provided consistent ecological interpretations, concurring with what is thought to be true about Burrowing Owl ecology.

In terms of predictive ability alone, RSFs were proportional to the probability of use as defined by the CWS Burrowing Owl locations, while ENFA models were not. Both methods produced significant chi-square values, indicating that neither method produced a model that fit particularly well with the expected data. However, the lowest chi-square value for an ENFA model is over 10 times the highest chi-square value for a RSF model, suggesting that the RSF outperformed the ENFA. Previous studies (e.g., Brotons et al., 2004, Olivier and Wotherspoon, 2006) demonstrated that logistic regression models tend to provide more accurate predictions than ENFA models, especially when absence data is available and reliable. My research indicates that RSFs also provide a more accurate prediction of suitable habitat than ENFA models when absence data are not available.

A preliminary step in multivariate logistic regression applications that is encouraged by Hosmer and Lemeshow (2000) is to assess variables for collinearity because the inclusion of correlated variables could produce spurious results. In practice, the cut-off point for designating variables as collinear typically ranges from 0.5 – 0.9, although 0.70 is frequently used in RSFs (e.g., Richardson et al., 2005). However, my results suggest that incorporating correlated variables up to a 0.90 threshold did not affect the predictive ability of RSF models. While reliable ecological information is still an asset to all modelling procedures, these results allow for more confidence in exploratory procedures for prediction, with less *a priori* knowledge.

Regarding the predictive patterns of both SDM techniques, I expected that ENFA models would be unaffected by the number of covariates and collinearity because the analysis is designed to take any number of correlated variables and transform them into fewer uncorrelated factors (Hirzel et al., 2002). The ENFA also weights the variables, without rejection, so that subjective decisions based on *a priori* knowledge are minimal (Hirzel et al., 2002). For the RSF models, I expected that the number of covariates and collinearity would affect their predictive ability, as regression analyses are typically affected by collinearity and redundancy (Bonate, 1999; Hosmer and Lemeshow, 2000).

However, in my study, the predictive ability of ENFA models, and not the RSFs, corresponded to the number of variables included in the analysis and the level of collinearity among the covariates. While these results are surprising at first, I argue that this relationship is related to ENFA's overall lack of predictive power. ENFA is designed as an optimal exploratory tool to detect species' niche characteristics and not for prediction (C. Calenge, pers. comm.). The basic principle behind the factor analysis is that any number of variables can be 'collapsed' into uncorrelated factors, thereby eliminating collinearity among variables in order to capture the main characteristics of the species' niche. These factors likely do not capture all of the variation that could be explained by the original covariates, and varying amounts of specific information can be lost. This decreases the predictive power of the analysis in order to generalize the species niche. This problem is potentially exacerbated by increasing the number of covariates, regardless of their collinearity, as this can increase the statistical 'noise' or redundant information in the analysis. Because the increased information and noise are collapsed together, variation is lost while redundant information is included; causing decreased

predictive power with a greater number of covariates. The RSF technique is different, as it captures and uses all of the information that is provided by the data. By incorporating all of the specific details and information, RSFs provide more accurate predictions, regardless of the variable set used.

Predictive ability, however, is not the sole measure of model performance. Basille et al. (2008) emphasize two questions fundamental to habitat selection studies: the where-question of prediction ("Where is the species found?") and the what-question ("What does the species search for?"). Often the focus is on prediction, but we must also look at the ecological relationships revealed in the model. ENFA models provided robust, ecologically meaningful marginality coefficients corresponding with previous research on Burrowing Owl habitat requirements, regardless of the number of variables and collinearity in the analysis. In the RSF models, however, the strength and direction of certain variable coefficients changed depending on the variable set. These inconsistent coefficients are known as 'bouncing betas', or unstable model parameters. While the RSF models were accurate predictors, these bouncing betas indicate that the number of variables and collinearity present in the models does affect model performance. This bouncing beta phenomenon can be problematic for biologists and managers trying to determine and identify what specific environmental characteristics provide suitable habitat for the species in question.

An example of this problem is seen in Figure 2.3. For all RSF models, Burrowing Owls selected urban areas consistent with anthropogenic land uses (e.g., Moose Jaw and Regina are ranked highly suitable, as indicated by the dark green colour in Figure 2.3). The implications of designating *all* human land use areas as suitable habitat is potentially

quite devastating to the recovery of the species. While Burrowing Owls are adaptable and can occur on small patches of vegetation as long as there is a burrow, selecting for this entire land use is highly unlikely. A more likely explanation is that the proportion of human land use is extremely small over the entire landscape (~0.55%) and there are a number of notable owl locations in anthropogenic areas; specifically, golf courses and pastures near horse racetracks in Moose Jaw. As well, certain vegetative areas such as those near farmstead or roadside ditches may have been lumped into the urban land-use category (PO), due to data constraints (pixel size of 30x30m). This could also create confusion between the 'used' vegetated areas, and the 'unused' road or building within the pixel. The RSF method uses this information by designating this 'rare' land-use as being highly selected for, as the proportion of used points is significantly greater than the proportion of 'other' land use in the available environment. However, ENFA models show that this relationship is insignificant, with a median marginality coefficient value close to zero. ENFA recognizes that 'other' land-use is rare over the entire landscape and may not be an important overall indicator of species' habitat suitability. While RSF appears to be highly affected by a small number of points, outliers do not significantly affect the ecological interpretability of ENFA models. The vegetated areas within urban land-use may be important, however, only a small pixel size (grain) would be able to tease apart these relationships more thoroughly.

Another issue confounding this analysis is the existence of non-linear relationships between predictor variables and species locations, which could affect each SDM techniques quite differently. Hirzel et al. (2002) caution that the "ENFA only handles linear dependencies within the species niche." As such, I did not include or

account for non-linear relationships, as my goal was to compare modelling techniques under the most similar conditions. However, in chapter 3, I show that most of the relationships between Burrowing Owl use and the environmental predictor variables can be described by non-linear terms. This means that the linearity assumptions of the ENFA are inappropriate for this analysis, which could explain the lack of predictive power. The RSF technique allows for some adjustment if collinearities and/or non-linear relationships are present, which may account for the higher predictive power in conjunction with the bouncing betas. However, by exploring the nonlinearities explicitly, RSFs may yield consistent and interpretable ecological patterns, while retaining the high predictive ability.

Another factor that could create problems with model performance is the non-random collection of points within the provincial databases. Burrowing Owls near human land-use areas are probably more likely to be seen and reported, as opposed to owls that are located within large pastures less-disturbed by humans. Mackenzie et al. (2006) outlined principles and methods dealing with detection issues; however, because my study is comparing two techniques using the same data, detection problems are inherent in all derived models, regardless of technique.

Overall, these results support previous research that attests to ENFA's utility as a preliminary step in habitat modelling. Hirzel et al. (2001) showed that ENFA models were robust to the quality and quantity of the data, when using a virtual species under controlled conditions. Olivier and Wotherspoon (2006) suggest that ENFA predictions can provide a template for characterizing habitat suitability before the application of other modelling techniques and this analysis supports that observation. However, I believe that

RSFs have a greater potential to overcome the statistical issues present in this study. My goal was to create simple habitat suitability models to compare modelling techniques under the most similar conditions, and I found that RSFs were highly predictive models. An assessment and incorporation of non-linear relationships in future studies can alleviate the problem of bouncing betas. As well, there are model selection techniques available for use with RSFs that are useful for evaluating specific *a priori* predictions of habitat suitability, and significant variable sets. At the very least, an examination of the ecological interpretations of the ENFA models can provide a useful starting point for developing RSF models and predictions.

2.5 CONCLUSION

My comparison of two SDM techniques revealed that ENFA models can provide robust ecological indications of habitat suitability, while a carefully designed RSF model can provide better spatially-explicit predictions. ENFA models were poor predictors overall, and the predictive ability of these models increased as the number of covariates and level of collinearity decreased. RSF models were all good predictors, and their predictive ability was less affected by changing the number of covariates included. However, ENFA models provided consistent ecological interpretation corresponding to previous research for the species. The ecological interpretations of the RSF were inconsistent, shown by large changes in coefficient values and some spurious relationships from high to low collinearity levels. Endangered species biologists contend with real species and real data, and I provide an example using real data where the effects of multiple variables and collinearity are considered in relation to both the predictive ability and ecological implications of two different SDM techniques.

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[1] The Swift Fox DEM project relied on four data sources: Saskatchewan National Topographic Series 1:50,000 (NTS50) 20m dems, Alberta NTS50 20m dems, US Shuttle Radar Topography Mission (SRTM) 26m (1 second arc), and SRTM 75m (3 second arc).

Table 2.1. Environmental predictor variables used as the basis for all ENFA and RSF model building. Each variable is represented as a raster layer with a 30-m resolution, where each pixel is a focal summary of the surrounding area within a 1.2-km radius. "b" indicates layers that were transformed in BIOMAPPER 3.2 software (Hirzel et al., 2006) using the Box-Cox algorithm (Sokal and Rohlf, 1981).

Code	Environmental Predictor Variable, units	Mean	SD	Min.	Max.
EL	Elevation, m	772.3	136.5	497	1443
SL	Slope, degrees	1.78	1.78	0	23.17
DR	Distance to roads, m	713	778	15	9846
DTV	Distance to tall vegetation (trees & shrubs), m	2318	3440	0	29716 *
DWA	Distance to water, m	1744	1593	0	14266 *
DWE	Distance to wetlands, m	2599	3986	0	36880 *
GE	Grassland edge density, m/km^2	2124.1	2747.9	0	21670 *
GN	Number of grassland patches	5.7	12.5	0	180
GP	Grassland patch size, m^2	1304693	1700936	0	4521600 *
GR	Grassland edge to area ratio	42.6	84.2	0	658
PC	Proportion of cultivated land	0.515	0.381	0	1
PG	Proportion of grassland	0.400	0.374	0	1
PH	Proportion of hay[b]	0.017	0.044	0	0.293
PO	Proportion of other land use (urban, roads, buildings) [b]	0.005	0.019	0	0.293
PS	proportion of shrubs [b]	0.012	0.028	0	0.287
PT	proportion of treed areas [b]	0.002	0.012	0	0.292
PWA	proportion of water [b]	0.013	0.036	0	0.293
PWE	proportion of wetland	0.016	0.032	0	1
RD	weighted road density, m/km^2	1359.6	1760.1	0	70444

** These layers possess values that were too large to compute within BIOMAPPER, therefore, they were divided by a factor to ensure maximum values < 10000 for each ENFA model.*

Table 2.2. Correlation matrix calculated between all environmental predictor variables across the entire study area using BIOMAPPER 3.2 software (Hirzel et al., 2006). All collinearities > 0.50 are highlighted in bold, italic font.

	EL	SL	DR	DTV	DWA	DWE	GE [c]	GN	GP [b]	GR	PC [a]	PG	PH	PO [c]	PS	PT	PWA	PWE	RD
EL	1																		
SL	0.34	1																	
DR	0.24	0.22	1																
DTV	0.18	-0.12	0.07	1															
DWA	0.21	0.06	0.1	0.35	1														
DWE	0.42	0.02	0.15	0.33	0.28	1													
GE	-0.06	0.31	0.02	-0.27	-0.13	-0.16	1												
GN	-0.14	0.02	-0.1	-0.18	-0.15	-0.13	***0.59***	1											
GP	0.31	0.24	0.48	0.17	0.18	0.15	-0.14	-0.27	1										
GR	-0.22	-0.24	-0.19	-0.03	-0.06	-0.1	-0.24	-0.07	-0.37	1									
PC	-0.25	-0.35	-0.48	-0.04	-0.06	-0.09	-0.28	0.05	***-0.79***	0.48	1								
PG	0.3	0.35	0.49	0.09	0.14	0.12	0.16	-0.13	***0.89***	-0.48	***-0.94***	1							
PH	0.01	-0.08	-0.11	0.01	-0.01	0.1	0.05	0.07	-0.16	-0.05	-0.07	-0.13	1						
PO	-0.11	-0.07	-0.13	-0.07	-0.09	-0.09	-0.03	0.01	-0.16	0.1	0.09	-0.18	-0.01	1					
PS	-0.14	0.22	0.06	-0.26	-0.11	-0.13	***0.74***	0.42	-0.11	-0.1	-0.24	0.12	0.01	-0.03	1				
PT	0.14	0.27	0.03	-0.12	0.03	-0.01	0.32	0.17	-0.05	-0.05	-0.14	0.06	-0.02	-0.02	0.23	1			
PWA	-0.12	0	0.11	-0.06	-0.31	-0.03	0.07	0.01	-0.07	-0.02	-0.19	-0.02	-0.01	-0.01	0.06	0.02	1		
PWE	-0.17	-0.02	-0.05	-0.16	-0.2	-0.29	0.25	0.14	-0.19	0.06	0.04	-0.14	-0.07	0.02	0.1	0.04	0.1	1	
RD	-0.11	-0.16	-0.36	0.01	-0.04	0	-0.05	0.03	-0.25	0.12	0.21	-0.27	0.1	***0.66***	-0.08	-0.03	-0.06	-0.02	1

Note that [a] indicates the highest collinearity (>0.90) variable removed at all lower levels, [b] indicates the strongest collinearity (0.75-0.90) variable removed at lower levels, and [c] indicates the weakest collinearity (0.5-0.75) variables removed at the lowest level.

Table 2.3. Modelling framework used to build all Ecological Niche Factor Analysis (ENFA) models and logistic regression Resource Selection Functions (RSFs), showing subsequent variable removals at each level with a reduced amount of collinearity. At the high collinearity level, all variables were retained. At the strong collinearity level (and subsequent lower levels), one variable was removed for every pair of variables correlated above the threshold value shown in the table (i.e. 0.90 at the strong level; see Table 2.2 for correlation values). Correlated variables were chosen at random for removal.

Collinearity Category	ENFA Variables *	ENFA model	RSF Variables **	RSF model
1) HIGH	(all 19 variables)	ENFA1a	F (all 19 variables)	RSF1a
	(all 19 variables) - R	ENFA1b	SW (all 19 variables)	RSF1b
2)STRONG	(19 - PC)	ENFA2a	*F* (19 - PC)	RSF2a
<0.90	(19 - PC) - *R*	ENFA2b	*SW* (19 – PC)	RSF2b
3) WEAK	(19 - PC - GP)	ENFA3a	*F* (19 - PC - GP)	RSF3a
<0.75	(19 - PC - GP) - *R*	ENFA3b	*SW* (19 - PC - GP)	RSF3b
4) LOW	(19 - PC - GP - GE - PO)	ENFA4a	*F*(19 - PC - GP - GE - PO)	RSF4a
<0.50	(19 - PC - GP - GE - PO) - *R*	ENFA4b	*SW* (19 - PC - GP - GE - PO)	RSF4b

** R = redundant variables defined by an absolute value < 0.05 for the marginality factor coefficient. These variables were removed to create a more parsimonious model comparable to stepwise logistic regression models.*

*** F = forced logistic regression model including all variables listed and SW = stepwise algorithm used to remove any non-significant variables from model*

Table 2.4. Predictive accuracy statistics (linear regression, χ^2 goodness-of-fit tests, and area-adjusted frequency Spearman rank scores) comparing expected values (derived from provincial database locations) vs. observed values (Canadian Wildlife Service data, n=359) for Burrowing Owls across the Canadian prairies. The most predictive model within each technique is indicated with "*".

a) Ecological Niche Factor Analysis (ENFA) models, ENFA1a – ENFA4b.

Collinearity Category	MODEL	Linear Regression			Goodness-of-Fit		Spearman (AAF)	
		R^2	β_0	β_1	χ^2	P	R_S	p
1) HIGH	ENFA1a	0.001	0.098	0.016	790.7	< 0.0001	0.346	0.328
	ENFA1b	0.002	0.097	0.026	785.7	< 0.0001	0.127	0.726
2)STRONG	ENFA2a	0.217	0.082	0.181	552.5	< 0.0001	0.491	0.150
	ENFA2b	0.096	0.090	0.100	591.9	< 0.0001	0.382	0.276
3) WEAK	ENFA3a	0.259	0.072	0.284	417.7	< 0.0001	0.491	0.150
	ENFA3b	0.257	0.074	0.256	379.6	< 0.0001	0.564	0.090
4) LOW	ENFA4a*	0.331	0.072	0.275	417.3	< 0.0001	0.600	0.067
	ENFA4b	0.370	0.074	0.262	551.1	< 0.0001	0.576	0.082

b) Logistic Regression-Resource Selection Function (RSF) models, RSF1a – RSF4b.

Collinearity Category	MODEL	Linear Regression			Goodness-of-Fit		Spearman (AAF)	
		R^2	β_0	β_1	χ^2	p	R_S	p
1) HIGH	RSF1a	0.899	0.018	0.817	35.5	< 0.0001	0.952	0.000
	RSF1b	0.904	0.018	0.815	34.0	< 0.0001	0.997	0.000
2)STRONG	RSF2a	0.958	-0.010	1.098	21.7	0.0099	0.997	0.000
	RSF2b	0.947	-0.008	1.082	24.3	0.0039	0.988	0.000
3) WEAK	RSF3a	0.963	-0.013	1.129	21.0	0.0125	0.988	0.000
	RSF3b*	0.966	-0.012	1.124	19.8	0.019	0.997	0.000
4) LOW	RSF4a	0.926	0.016	0.845	31.1	0.0003	0.988	0.000
	RSF4b	0.922	0.014	0.858	33.2	0.0001	0.979	0.000

Table 2.5. Variable and factor statistics for the Ecological Niche Factor Analysis (ENFA) model with the best predictive ability, ENFA4a. Shown below are the explained specialization values (in parenthesis) for the first 6 out of 17 ecological factors (marginality + five specialization factors) and coefficient values for the environmental predictor variables. Only the first 3 factors were retained to calculate the habitat suitability map, explaining 76.7% of the total information, and 53.5% of the specialization.

Variable	Marginality (12.1%)	Spec. 1 (33.8%)	Spec. 2 (7.6%)	Spec. 3 (6.5%)	Spec. 4 (5.8%)	Spec. 5 (4.7%)
SL	-0.55	-0.153	-0.64	-0.422	0.192	-0.188
DTV	0.385	0.025	-0.03	0.071	0.048	-0.119
PG	0.362	0.018	-0.265	-0.101	0.225	0.091
EL	-0.302	-0.004	0.654	-0.213	0.106	0.148
DR	-0.283	-0.063	-0.146	0.228	-0.696	0.179
PS	-0.276	-0.14	0.086	0.767	0.501	0.252
RD	0.235	0.013	-0.133	-0.06	-0.143	0.042
GR	-0.205	-0.022	0.117	-0.026	0.057	0.033
PT	-0.181	0.974	-0.046	0.059	-0.07	0.065
GN	-0.152	-0.034	0.095	-0.102	-0.075	-0.765
PWE	-0.11	-0.039	-0.008	0.021	0.064	0.418
DWE	0.054	0.018	-0.114	0.107	-0.042	0.062
DWA	0.025	-0.012	0.036	0.016	-0.027	0.016
PH	0.015	0.015	-0.059	-0.131	-0.086	0.055
PWA	-0.035	0.003	-0.053	0.272	-0.339	-0.225

Variables are sorted by decreasing absolute values on the marginality factor. Positive values on the marginality factor indicate that Burrowing Owl suitability increases with higher values than average for that variable, and vice versa. Coefficient signs on the specialization factor have no meaning, although large absolute values indicate some sensitivity to change.

Table 2.6. Variables in the Logistic Regression Resource Selection Function (RSF) model RSF4a. Variables were standardized before inclusion in model, to provide a direct coefficient comparison with ENFA4a. Shown below are the coefficients with standard errors and p-values for each term included in the model. Changes in coefficient ranks, the strength of association and the absolute values in comparison to the values for ENFA4a (illustrated in Table 2.6) are also provided for ease of interpretation.

Variable	Coefficient	SE	p	Δ Rank	Strength	Value
SL	-0.708	0.043	0.00	0	↑	0.158
PG	0.538	0.026	0.00	1	↑	0.176
DR	-0.500	0.041	0.00	2	↑	0.217
EL	-0.261	0.031	0.00	0	↓	0.041
PS	-0.222	0.037	0.00	1	↓	0.054
GR	-0.146	0.029	0.00	2	↓	0.059
DTV	0.124	0.021	0.00	-5	↓	0.261
DWE	0.106	0.027	0.00	4	↑	0.052
PT	-0.096	0.056	0.09	0	↓	0.085
DWA	-0.071	0.025	0.01	3	↓	0.096
RD	0.046	0.015	0.00	-4	↓	0.189
PWA	0.021	0.024	0.38	3	↓	0.056
GN	-0.016	0.027	0.55	-3	↓	0.136
PWE	0.014	0.023	0.54	-3	↓	0.124
PH	0.013	0.021	0.52	-1	↓	0.002

Variables are sorted by decreasing absolute values of the coefficients.

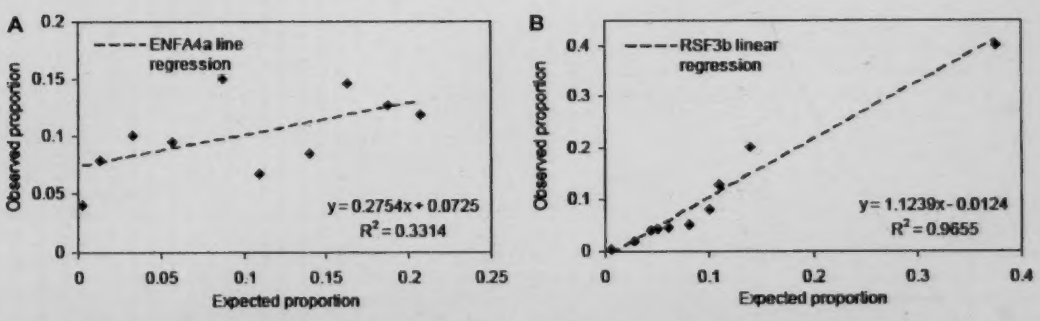

Figure 2.1. Expected versus observed proportion of evaluation data points for the temporally independent Canadian Wildlife Service data (n = 359) for A) the ENFA model with the highest predictive ability, ENFA4a, and B) the RSF model with the highest predictive ability, RSF3b. The fitted regression line is presented as a linear equation along with R^2 values.

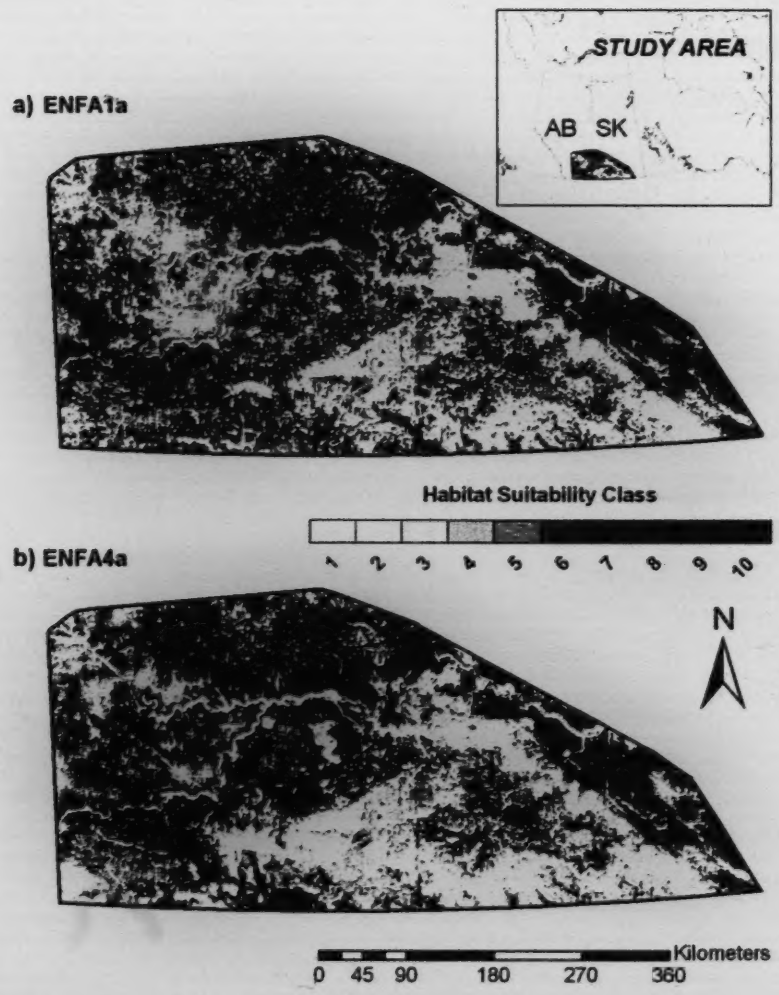

Figure 2.2. Ecological Niche Factor Analysis (ENFA) habitat suitability maps for Burrowing Owls across the Canadian mixed grassland prairies. The ENFA model with the least predictive ability according to Table 2.4 is shown in a) ENFA1a, while the ENFA with the most predictive ability is shown in b) ENFA4a. The inset map shows the study area located in southern Alberta (AB) and Saskatchewan (SK) in Canada.

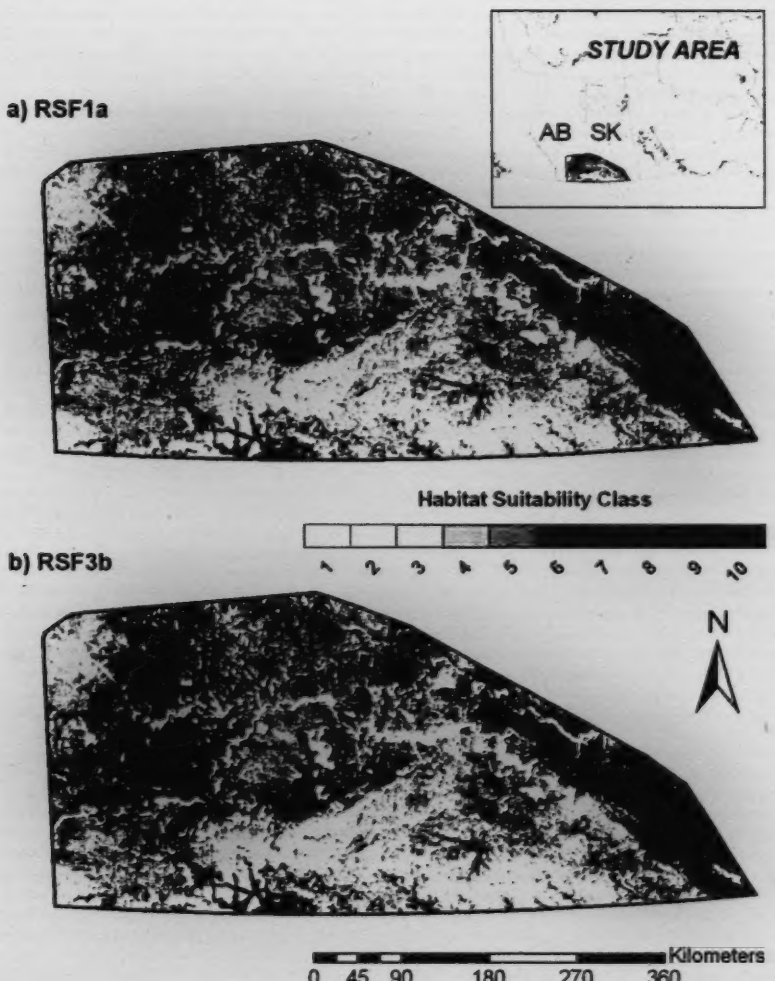

Figure 2.3. Logistic Regression Resource Selection Function (RSF) habitat suitability maps for Burrowing Owls across the Canadian mixed grassland prairies. The RSF model with the least predictive ability according to Table 2.4 is shown in a) RSF1a, while the RSF with the greatest predictive ability is shown in b) RSF3b. The inset map shows the study area located in southern Alberta (AB) and Saskatchewan (SK) in Canada.

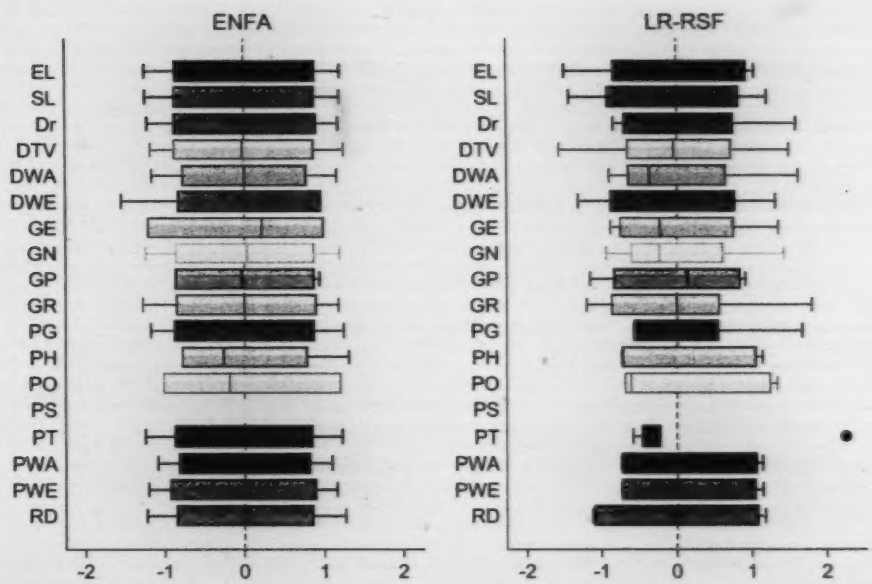

Figure 2.4. Box-plots of standardized coefficient values for each environmental predictor variable (excluding proportion of cultivated land, PC) included in all ENFA and RSF models. Median values close to zero and symmetric boxes about the median line indicate less variation over all models with differing collinearity levels. Median values furthest away from zero indicate coefficient instability.

CHAPTER 3. DO LARGE-SCALE ABIOTIC FACTORS INFLUENCE WHAT IS BIOTIC HABITAT FOR BURROWING OWLS IN THE CANADIAN PRAIRIES?

3.1 INTRODUCTION

Analysing species-habitat relationships is a key step in conservation planning for avian species. However, most studies that attempt to understand these species-habitat relationships are conducted at relatively small spatial scales in localized regions (e.g., Bisson and Stutchbury 2000, Davis, 2005; Stenhouse et al., 2005; Smith et al., 2007) describing third-order selection processes (Johnson, 1980). In general, these research projects have concluded that vegetation structure and composition are key determinants of avian habitat suitability. These conclusions have lead managers to focus on maintaining and manipulating vegetation as methods of conserving species, yet the importance of environmental abiotic factors in structuring vegetation communities (Clements, 1936; Whittaker, 1953) is often overlooked. Regional patterns in climate, soil, and biota are interdependent (O'Neill et al., 1986), and small-scale datasets do not reflect the variation produced by large-scale environmental processes that dictate higher order selection patterns (Johnson, 1980). Bio-geographical studies that examine the entire range of a species tend to find that abiotic environmental variables – such as climate and soils – are better predictors of where species occur (Turner, 2005).

Parker and Bendix (1996) reviewed multiple examples of how abiotic processes influence the distribution of vegetation at the landscape scale. Less is known about whether soil type or climate creates unique habitat conditions that are independent of

vegetation structure and composition. Understanding if climate and soils create unique habitat conditions for wildlife, beyond the effects they have on vegetation, is important to managers charged with identifying critical habitat for several reasons. First, management strategies designed to maintain non-hunted species are often limited to policies that manage for optimal vegetation structure via different land-uses. If climate and soils are bigger drivers of wildlife use, there is less ability for managers to alter these conditions. Second, much of the variation between local studies may occur because vegetation models created in one region do not apply in a different climatic or soil regime. Blanket prescriptions that apply one definition of optimal vegetation structure across the entire range of a species may not be the best conservation practice.

One example of the difficulties of defining critical habitat based on vegetation structure alone exists for the Burrowing Owl. Most studies have quantified fine-scale vegetation requirements for nest- and foraging-site selection in Burrowing Owls (third-order selection; Johnson 1980). A perusal of the literature shows considerable variation in the conclusions drawn from these studies, making the qualitative descriptions that have been used thus far by the Burrowing Owl recovery team insufficient for planning purposes. For example, Burrowing Owls have been found to preferentially select nest burrows in grassland pastures and avoid crop fields in the Regina Plain (Poulin et al., 2005). In Idaho, nests were closer to roads and irrigated crop fields than would be expected by chance (Rich, 1986; Beltoff and King, 2002). Some studies have shown that owls prefer to nest in areas with higher densities of fossorial mammal burrows but others have shown no effect (Beltoff and King, 2002; Poulin et al., 2005; Lantz et al., 2007; see Schmutz, 1997 for no difference). Burrowing Owls selected foraging sites in areas that

were low-lying, ephemeral wetlands and edges rather than intact grassland in the Eastern Irrigation District in southern Alberta (Sissons, 2003). A similar study within the heavily-cultivated region of Saskatchewan found that owls avoided cropland and fallow, and preferred foraging in the core of their nesting pastures (Sissons et al., 2001). Several years previous in the same province, pasture and crop areas were avoided by owls and selection was for human-modified grass-forb vegetation that is typical of road rights-of-way (Haug and Oliphant, 1990). The one commonality of Burrowing Owl nest- and foraging-site selection studies is that the owls appear to be ambiguous to or possibly prefer landscape heterogeneity. An alternative hypothesis is that the variation in habitat selection seen across the range of the Burrowing Owl results from differences in abiotic processes at a larger scale, i.e. those processes that occur at a higher order of selection.

In this chapter, I present logistic regression resource selection functions (RSFs) created over the current natural breeding range of the Burrowing Owl, representing ~18 million hectares of mixed prairie grassland in Alberta and Saskatchewan. My objectives were to: 1) determine the relative importance of abiotic factors (i.e. soils, climate, and geography) relative to biotic vegetation factors (land-use and fragmentation) as predictors of second-order (home-range) habitat selection; and 2) evaluate whether owls selected the same vegetation conditions across a gradient of abiotic conditions. Specifically, I identified the most predictive set of environmental variables associated with Burrowing Owl home-range selection, and determined if the importance of vegetation factors changed in relation to the most predictive abiotic processes. To do this, I classified 37 environmental predictor variables into five categories: geography, land-use, grassland fragmentation, soil, and climate. I created RSFs for each set of variables and evaluated

the predictive ability of each RSF. I then examined interaction effects to determine whether or not the relationship between vegetation variables and the probability of owl home-range selection varied within large-scale abiotic categories.

3.2 METHODS

3.2.1 Species Location Data

I developed all models with data provided by provincial databases: the Alberta government's Fish and Wildlife Management Information System (FWMIS) and the Operation Burrowing Owl (OBO) program in Saskatchewan. I supplemented this data with observations from other independent sources and removed duplicates. These data were constrained to the study area extent, and only included points from 1987-2002. These data consist of presence-only observations (with no reference to absence), where observers detected Burrowing Owl presence either visually or indirectly (e.g., food pellets located near burrows). Data accuracy varied up to a maximum of a quarter-section (800m x 800m or 64 ha); therefore, I randomly selected one 'used' point within each 'used' quarter section. To quantify the available landscape, I generated random points across the landscape, excluding any water bound areas. These 'available' points provided the set of comparison points for all statistical analyses.

A second, temporally independent dataset of 'used' points was provided by the Canadian Wildlife Service and used for model evaluation. These data were collected from 2003-2006 for a Burrowing Owl nest monitoring project undertaken by T. Wellicome. Burrowing Owl nests and other incidental presence-only detections were located through surveys of known breeding areas, and by searching the surrounding

landscape. Additional locations were obtained through cooperation with other biologists, land owners and managers with knowledge of breeding Burrowing Owl locations.

3.2.2 Environmental Data

I measured 37 variables using ArcGIS 9.x (ESRI, 2004). I derived a spatial raster layer for each variable with a 30-m pixel resolution over the entire study area (see Table 3.1 for a detailed summary of variables and data sources). Haug and Oliphant (1990) found that the maximum home-range size for a Burrowing Owl was approximately 4.8-km^2; therefore, I summarized all variables within a 1.2-km radius moving window across the landscape.

I created five classes of variables to model the spatial distribution of Burrowing Owl home-range selection: geography, grassland fragmentation, land-use, soil characteristics, and climate. I created these classifications to examine the importance of land-use and grassland fragmentation (vegetation management factors) in comparison to abiotic factors that cannot be easily manipulated by managers – geography, climate, and soil characteristics. These five classifications also allowed for smaller sets of similar variables to be examined and simplified, in order to obtain the most parsimonious global model.

Geography considers four variables: elevation, slope, and spatial location in terms of a false easting and northing. I used spatial location as a surrogate for unmeasured spatial gradients, scaling each variable down by a factor of 100,000 before inclusion. Burrowing Owl habitat is typically associated with low, flat areas (Wedgwood, 1978; Haug et al., 1993); I therefore included focal summaries of elevation and slope as covariates.

For grassland fragmentation, I examined four variables: overall edge density, area-to-edge ratio, number of patches, and mean patch size within the home-range radius. Within the land-use class, I included features such as water, wetland and tall woody vegetation (trees and shrubs). I created proportional rasters that quantified the amount of specified land-use within the home-range surrounding each focal cell. Previous studies have also looked at distance to land-use as variables; therefore, I included distance to tall woody vegetation, wetlands, and water.

The importance of soil characteristics was demonstrated by Harris and Lamont (1985), who found that historical Burrowing Owl locations were correlated with land systems (soil groups and landforms). As their soil classification system differed slightly from the current Canadian Soil Classification System, I described soil in terms of the dominant soil orders and parent materials and texture found in the region, and quantified these characteristics using proportional rasters.

Climate is considered to be one of the main drivers of overall landscape patterns (O'Neill et al., 1986; Turner, 1989), and subsequently, species distribution (Turner, 2005). For climate, I considered average precipitation and minimum and maximum temperatures for the months of March, April, and May. This period coincides with Burrowing Owl migration into the study region. A recent analysis of habitat within the Regina Plain in Saskatchewan found that the average monthly precipitation in March was important to predicting owl distribution (E. Svendsen, pers. comm.).

3.2.3 Statistical Modelling

All statistical analyses were conducted in STATA 9.0 (STATA corp., 2005). Before multivariate analysis, I used Generalized Additive Models (GAMs) to determine

the shape of the relationship between each variable and owl use. Results were graphed and examined visually for non-linear relationships. If non-linear relationships were observed, I created univariate logistic regression models to compare the linear relationships with non-linear functional forms (quadratic, cubic, exponential, logistic, threshold breakpoints). A dichotomous variable was included when frequency distributions indicated a disproportionate amount of 0 values ($d = 0$ if $x = 0$, $d = 1$ if $x > 0$; Hosmer and Lemeshow, 2000). I compared these univariate relationships of each variable to previous knowledge of Burrowing Owl ecology, and incorporated different functional forms into the modelling framework. In Chapter 2, I found that the inclusion of correlated variables up to a maximum of 0.90 did not significantly alter the predictive ability of logistic regression RSFs. Therefore, I calculated a Pearson correlation matrix between all variables to test for potential collinearities, and examined all models for inflated standard error estimates.

I used a logistic regression Resource Selection Function (RSF; Manly et al., 2002) framework to model Burrowing Owl distribution as a function of the five classes of variables described above. I consider distribution to be the relative probability of Burrowing Owl home-range selection (second-order selection; Johnson, 1980). Used (1) and available (0) points were sampled at the population level (design I RSF), and compared using the logistic discriminant:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

where w(x) is the RSF estimating relative likelihoods, and $\beta_1 \ldots \beta_n$ represent the coefficients estimated from a logistic regression model (Manly et al., 2002; Johnson et al., 2006).

For each of the 5 classes of variables, I created two RSF models: the global (designated by subscript 'g') model that included all variables with appropriate different functional forms and a final reduced and simplified (designated by subscript 'rs') model. To create the simplified model, I used a backwards elimination process to systematically test global models for a reduction in the number of terms (removal of each variable in it's entirety) and a simplification of complex non-linear terms (e.g., from cubic to quadratic to linear). I employed an information-theoretic process (Burnham and Anderson, 2002) and examined Akaike's and Bayesian Information Criteria (AIC and BIC) values at each step, selecting models with a reduction >10 in AIC and BIC values. I also created one 'all-inclusive' model that combined all 5 simplified models, for a total of 11 RSFs. I extrapolated each RSF to the study area using ArcGIS 9.x software (ESRI, 2004) to produce Burrowing Owl distribution maps depicting the relative probability of home-range selection.

3.2.4 Model Evaluation

Model evaluation was done as per methods outlined in Chapter 2.

3.2.5 Interaction Assessment

I determined that soil and climate variables produced the most predictive large-scale models for Burrowing Owl selection. Therefore, I summed the RSF rasters for the simplified models for soil and climate, and created a soil/climate raster map. I re-classified the map using equal area breakpoints into 3 levels illustrating relative probabilities of owl home-range selection, as predicted by soil and climate conditions alone (low to high, 1-3). I intersected all used and available points with this raster to

create a soil/climate categorical variable, and I examined vegetation management variables in combination with the soil/climate variable for interactions. Specifically, I looked at variables that could be altered using common land-management practices in farming and ranching activities. To assess interaction effects, I created two models (one with, and one without, an interaction term) for each vegetation-management variable and examined the change in AIC and BIC values between models. Each (continuous) variable with the potential of an interaction was reclassified into a categorical variable. Selection ratios (Manly et al., 2002) were examined and graphed for a visual illustration of the relative probability of use at each of the three soil/climate levels. I calculated the selection ratios using the following formula:

$$\hat{w}_i = o_i / \pi_i$$

where $\hat{w}_i$ is the selection ratio for a given resource category i, expressed as the ratio of the sample proportion of used units, o_i, to the sample proportion of available units, π_i.

3.3 RESULTS

I assembled 3689 Burrowing Owl locations from the provincial data from 1987 to 2002, and generated a set of 70,783 points that described the available landscape. Using these data in univariate analyses, the GAMs showed that the relationship between Burrowing Owl home-range selection and 35 of the 36 continuous variables are described by non-linear relationships. These non-linear relationships were incorporated into all 11 multivariate RSFs: two for each variable class set (global and simplified), and one all-inclusive model that encompassed all sets of variables. I removed the cultivated land variable (pCrop) from all models because of the high correlation between proportion of cultivated land and grassland ($r = -0.94$).

According to model selection (Information Criteria, IC) scores, the all-inclusive model (k=62) received the most support out of all models (e.g., 2236 AIC units better than the second best model, Table 3.2). Model ranking changed for out-of-sample evaluation, which compared the spatial predictions of Burrowing Owl selection to the actual CWS dataset locations (n=558; Table 3.2 and Figure 3.1). Out of the isolated models, soil characteristics produced the most predictive models, followed by climate and then geography. Land-use and grassland fragmentation models had the least predictive power. Spatial predictions of Burrowing Owl home-range selection for all simplified models and the all-inclusive model are shown in Figure 3.2.

I considered individual variables to be important descriptors of Burrowing Owl habitat selection when the *p* values remained at < 0.05 from the isolated to the final all-inclusive model and when the parameter estimates were stable (Table 3.3). In summary, Burrowing Owls were associated with flat, low areas (β^2_{Elev} = -5.098; β_{Slope} = -0.352), lower grassland edge densities (β_{gEdge} = -0.169), and a moderate grassland patch size (quadratic relationship; β_{gSize} = 0.075 + β^2_{gSize} = -0.039). Land-use distance variables were unimportant when all variables were considered. However, owls selected increasing proportions of grassland up to 0.25, which then stabilized based on a breakpoint functional form (β_{pGrass_25bp} = 6.309). Owls also selected areas with moderate amount of wetland as indicated by the better fit of a quadratic functional form (β_{pWet} = 17.315 + β^2_{pWet} = -75.404). Most soil variables remained important within the all-inclusive model, with owls associated with moderate proportions of chernozemic soils (quadratic function; β_{sCher} = 0.014 + β^2_{sCher} = -0.00015), decreasing levels of regosolic soils (β^2_{sRego} = -0.00027), increases in solonetzic soil up to 55% (breakpoint function; β_{sSolo_55bp} = 0.013),

slight increases in vertisolic soils ($\beta_{sVert} = 0.018$), and moderate associations with fluvial parent material (quadratic function; $\beta_{pmFluv} = -0.011 + \beta^{0.5}_{pmFluv} = 0.091$). Coarser, sandy soils were the most preferred texture compared to finer, clay soils ($\beta_{sText_6} = 0.665$; categorical variable for texture 6 with reference to texture 1). In terms of climate, moderate minimum temperatures in March, April, and May, and moderate maximum temperatures in April and May were the variables most strongly associated with Burrowing Owl home-range selection (Table 3.3).

Soil and climate predictions were combined to create the soil/climate variable (illustrated in Figure 3.3) to examine how specific vegetation management variables might vary among soil and climate conditions. Interaction effects were present for three of the five vegetation variables tested: pGrass, gEdge, and gSize (Table 3.4). Figure 3.4 shows that pGrass had a strong interaction with soil/climate, gEdge had a very weak interaction, and gSize had a moderate interaction. For pGrass, trends in the selection ratios change from negative (for soil/climate = 1 and 2) to positive (at soil/climate = 3). In all instances, owls selected against the lowest proportions of grassland (< 0.1) and selected for higher proportions up to 0.7. However, owls only selected for grassland proportions above 0.7 when they are in ideal soil and climate conditions (soil/climate = 3); otherwise, owls select against levels of grassland > 0.7. A similar trend is seen in gSize selection ratios, where there is a negative selection for the highest grassland patch sizes (above ~3.5 km^2) when soil/climate = 1 and 2 and a switch to positive selection when soil/climate = 3. Selection for gSize switched from negative to positive at ~0.110 km^2 (-2 on graph; Fig. 3.4) when soil/climate = 1 and 2, and ~ 0.343 km^2 (-1 on graph; Fig. 3.4) when soil/climate = 3. For gEdge, a negative trend is consistent, as owls

selected against the highest (~ 5 km/km^2 or greater) and lowest edge densities (> 0.1 km/km^2). The strongest selection for gEdge occurred at approximately 1-2 km/km^2. Note that 60% of all used points fall into the soil/climate = 3 category, so these points are driving the patterns seen over all soil/climate levels.

3.4 DISCUSSION

This study suggests that the best predictors of Burrowing Owl home-range selection in western Canada are large-scale abiotic factors. Soil characteristics produced the habitat selection model with the greatest predictive accuracy, followed closely by climate characteristics. Vegetation factors that can be more easily manipulated by managers (land-use and grassland fragmentation variables) had the least predictive power. As well, selection trends for 3 of the 5 vegetation variables changed depending on the soil and climate regime. These results indicate that the current habitat description – open prairie grasslands that are flat and treeless with sparse vegetation and burrows – does not fully encapsulate what owls truly require.

There are several potential reasons why climate and soil characteristics play an important role in Burrowing Owl habitat selection. First, climate is thought to be one of the major abiotic drivers of bio-geographic landscape patterns (O'Neill et al., 1986; Turner 1989). Climate variables were the main drivers of multiple species distributions across Europe at coarse scale resolutions (Thuiller et al., 2004; Luoto et al., 2007). Thuiller et al. (2004) also showed that temperature and precipitation gradients accounted for most of the explanatory power and spatial variation of land cover.

Climate and soil may also influence the agricultural practices and grassland distribution on the landscape, and subsequently dictate where owls obtain certain

resources. While my descriptions of the land-use cover types are coarse because of limited available data resolution (no information on species of grass for example), there is some evidence that cultivated areas can provide better foraging sites than non-cultivated sites. Prey biomass used by Burrowing Owls is dominated by vertebrates (Sissons, 2003; Poulin and Todd, 2006), and in Saskatchewan small mammals were more abundant in crops and right-of-way habitats than in pastures (Sissons et al., 2001; Poulin 2003). In Idaho, Burrowing Owls are thought to associate with irrigated cropland because of increased prey abundance and/or diversity compared to areas that are not cultivated (Rich, 1986; Moulton et al., 2006). It is unknown whether particular types of crops are more or less likely to have Burrowing Owl prey; however, certain soil conditions may allow for better production of seed-producing crops, which may then translate to higher densities of small mammals. As well, grassland species respond to differing soil conditions (Brown, 1943; Nixon and McMillan, 1964), and grassland structure and composition are known to influence small mammal populations (Rosenzweig and Winakur, 1969; Jones et al., 2003; Washburn and Seamans, 2007). However, exactly how this influences Burrowing Owl habitat selection remains untested.

Alternatively, soil conditions may simply be a surrogate measure for burrow availability, which is critical in determining whether burrows can occur (Coulombe 1971; Thomsen 1971; Haug et al., 1993). Burrowing Owls are unique in North America as they nest in abandoned, underground burrows, most commonly created by prairie dogs, ground squirrels and badgers (Haug et al., 1993; Poulin et al., 2005). Previous studies indicated that soil type has significant effects on burrow survival and re-use by owls in the Columbia Basin in Oregon (Green and Anthony 1989; Holmes et al., 2003).

McCracken et al. (1985) found that nest burrows had greater sand content, less silt content, and equal clay content than adjacent non-nest burrows. Although their results were not statistically significant, McCracken et al. (1985) suggest that the difference may still be biologically relevant, because sandy soils may facilitate burrow enlargement and drainage during floods. My results demonstrate selection for coarse-textured, sandy soils, and avoidance of finer, clay-like soils. Most likely, the dense nature of clay and clay-like soils from their small particle size (Soil Classification Working Group, 1998) are not conducive to burrow construction by fossorial mammals. Soil conditions that allow for more burrow construction are beneficial from an owls' perspective, because owls have sometimes been found to select nest sites in areas with higher ground-squirrel and prairie dog burrow densities (Poulin et al. 2005; Lantz et al., 2007). Apps et al. (2002) also showed that soil parent material, order and texture are associated with American badger (*Taxidea taxus*) use. This further strengthens the argument for soil as a surrogate measure, because badgers are one of the main providers of suitable nest burrows for Burrowing Owls (Green and Anthony, 1989; Poulin et al., 2005). However, this relationship needs to be clarified further in terms of survival and reproductive success for Burrowing Owls, because badgers are also known to be major predators of owls and their nests (Green and Anthony, 1989; Haug et al., 1993; Wellicome et al., 1997).

Historical Burrowing Owl declines have been attributed to loss and fragmentation of native grassland habitat in the Canadian Prairies (Haug et al., 1993; Wellicome and Haug, 1995; COSEWIC 2006). Therefore, I expected that land-use and grassland fragmentation would be important drivers of current owl distribution if owls are actively searching for and selecting the remaining parcels of intact grassland undisturbed by

farming. However, my results indicated that land-use and fragmentation were poor predictors of Burrowing Owl home-range selection across the Canadian Prairies. My objective was to define overall selection patterns, and I considered all covariates in Alberta and Saskatchewan to be equally available to all owls when I defined my available landscape. Though soil and climate regimes were evenly distributed across the landscape, vegetation patterns were not. Myerstud and Ims (1998) noted that habitat selection can be conditional on availability, and therefore, the importance of vegetation could be confounded by its availability on the landscape. Most of the intact, large parcels of grassland are found in Alberta in association with large-scale ranching. However, Saskatchewan is dominated by cultivated land, fragmenting the remaining grassland parcels and the entire landscape. The high degree of correlation found between the proportion of cultivated land (pCrop) variable and proportion of grassland (pGrass) variable illustrates this association. To explore this relationship more explicitly, it may be necessary to separate the available landscape according to the dominant land-use practice, and review habitat selection accordingly. However, Burrowing Owls have the ability to disperse large distances among years (e.g., from one province to another; Wellicome et al., 1997), so the assumption that all habitat is available to all owls may be a reasonable one.

An interesting result of this study was that most relationships between owl habitat selection and vegetation factors were non-linear in form. The best approach to grassland management within the Canadian Prairies is highly debated when considering recovery policies for Burrowing Owls. A common theme in prairie conservation is the preservation and restoration of grasslands: protecting or creating the largest patches

possible and maximizing grass height (Prairie PIF, 2004). While logical, some studies indicate that owls forage at edges, suggesting that landscape heterogeneity may be important. I showed that Burrowing Owls selected increasing amounts of grassland and larger grassland patches, but only in areas where soil and climate conditions predicted high selection by owls. Larger grassland patches within a good soil and climate regime might allow for heterogeneity within the grassland patch itself (e.g., well-grazed sites combined with overgrown sites allowing for owls to forage for small mammals). When soil and climate regimes are not optimal, the larger grassland patches may not provide enough heterogeneity, and therefore owls select moderately-sized patches that allow for other land-use (e.g., cultivation, wetlands) and edges for maximum foraging value. These changes in selection among soil and climate regimes may also relate to variation in grass-species composition and associated prey communities. Alternatively, owl nesting locations may reflect selection by burrowing mammals for landscape heterogeneity. Lastly, larger grassland patches could have greater burrow longevity that is dictated by the soil and climate regime as described above.

Unlike previous research on nest-burrow associations (Poulin et al., 2005), I found that owls were more likely to select moderate proportions of grassland within a simulated home-range. This discrepancy is potentially linked to the differences in scale: nest-burrow habitat is a finer scale of selection than home-range selection (third vs. second order; Johnson, 1980). Burrowing Owls may be placing their nests within grassland patches where burrows are available (Wellicome et al., unpubl. data), but foraging in other areas within their home-range where prey availability and hunting success are high (Sissons, 2003). This observation would partially explain the

discrepancies in habitat selection among scales and supports the hypothesis that Burrowing Owls prefer landscapes that are heterogeneous, at least at the home-range scale. Previous foraging studies (Haug and Oliphant, 1990; Sissons, 2003) conducted on a local scale showed that Burrowing Owls avoided both grassland pastures and cropland; however, there is a need for a foraging study that accounts for changes in large-scale environmental processes across the species' range.

3.5 CONCLUSIONS

My results show that the large-scale, abiotic factors of soil and climate can predict Burrowing Owl home-range selection and create unique habitat conditions for the owls, independent of vegetation, across the Canadian prairie breeding range. Vegetation may be an important predictor for habitat selection studies on a finer scale within varying soil and climate regimes. These models can be used by the recovery team to help target areas for critical habitat designation, although more information is needed to prioritize habitat across a range of abiotic conditions. Regardless of scale, abiotic factors and vegetation management must be considered in terms of nesting success and fledgling production. In the final chapter of my thesis, I explore these potential relationships, to determine if Burrowing Owl home-range selection is linked to reproductive success.

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Table 3.1. Environmental predictor variables used for Burrowing Owl habitat selection models in the grassland prairie region of Canada. The four letter codes identifying the five classes of variables are underlined in bold font.

Class	Code	Description and units	Data Source	Mean	SD
Geography	East[a]	false easting, m	Created using Spatial Analyst extension in ArcGIS 9.1.	384597	183006
	North[a]	false northing, m		192285	87757
	Elev	elevation, m	Digital Elevation Model (DEM) provided by Parks Canada (Swift Fox recovery team)[b]	772.3	136.4
	Slope	slope, degrees		1.775	1.784
Grassland **Fragmentation**	gEdge	grass edge density, km/km^2	Western Grain Transition Payment Program (WGTPP) landcover grid, Prairie Farm Rehabilitation Administration	2.124	2.748
	gPatch	number of grass patches		5.70	12.45
	gSize	mean patch size, km^2		1.305	1.701
	gRatio[a]	grass edge to area ratio		42.64	84.23
Land-Use	dTVeg[a]	distance to tall vegetation (trees & shrubs), m	Western Grain Transition Payment Program (WGTPP) landcover grid, Prairie Farm Rehabilitation Administration	2318	3440
	dWater[a]	distance to water, m		1744	1593
	dWet[a]	distance to wetlands, m		2599	3986
	pCrop	proportion of cultivated land		0.515	0.381
	pGrass	proportion of grass		0.400	0.374
	pHay	proportion of hay		0.025	0.080
	pShrub	proportion of shrubs		0.015	0.043
	pTrees	proportion of treed areas		0.003	0.025
	pWater	proportion of water		0.020	0.080
	pWet	proportion of wetland		0.016	0.031
Soil Characteristics	sCher	proportion of chernozemic order soils	Soil Landscapes of Canada v3.1. Agriculture and Agri-Food Canada. (Digital map and database at 1:1 million scale).	0.666	0.326
	sGley	proportion of gleysolic order soils		0.032	0.042
	sRego	proportion of regosolic order soils		0.045	0.135
	sSolo	proportion of solonetzic order soils		0.128	0.246
	sVert	proportion of vertisolic order soils		0.074	0.209
	pmEoli	proportion of eolian parent material soils		0.052	0.168
	pmFluv	proportion of fluvial (alluvial) parent material		0.079	0.164
	pmLacu	proportion of lacustrine parent material soils		0.258	0.322
	pmTill	proportion of till (moraine) parent material soils		0.494	0.364
	sText	categorical soil texture, from 1 (fine) to 7		---	---
Climate	Ppt3	average precipitation in March, mm	Worldclim database, version 1.4, http://worldclim.org	177.8	24.0
	Ppt4	average precipitation in April, mm		242.7	31.9
	Ppt5	average precipitation in May, mm		421.8	63.5
	Tmin3	minimum temperature in March, °C * 10		-101.7	12.5
	Tmin4	minimum temperature in April, °C * 10		-21.7	5.9
	Tmin5	minimum temperature in May, °C * 10		37.8	6.7
	Tmax3	maximum temperature in March, °C * 10		12.5	15.9
	Tmax4	maximum temperature in April, °C * 10		110.0	8.2
	Tmax5	maximum temperature in May, °C * 10		183.8	6.6

[a] *Variables were scaled down by a factor for all statistical analyses: 100000 for East and North, 10 for gRatio, and 10000 for dTVeg, dWater, and dWet.*

[b] *The Swift Fox DEM project relied on four data sources: Saskatchewan National Topographic Series 1:50,000 (NTS50) 20m DEMs, Alberta NTS50 20m DEMs, US Shuttle Radar Topography Mission (SRTM) 26m (1 second arc), and SRTM 75m (3 second arc).*

Table 3.2. Evaluation statistics of candidate models of Burrowing Owl home-range selection in the mixed grassland Canadian prairies, developed over the period 1987-2002. Model selection measures are presented for relative comparisons of model fit. Out-of-sample evaluation statistics evaluate predictive accuracy by comparing model predictions (expected values) with out-of-sample CWS data (observed values) collected from 2003-2006. Model selection rank is based on the lowest ΔAIC scores, while final rank of model predictive ability is based on Goodness-of-Fit tests, Spearman rank scores, and linear regression R^2 values (shown in Figure 3.1).

		MODEL SELECTION						OUT-OF-SAMPLE EVALUATION				
								Goodness-of-Fit		*Spearman (AAF)*		
Model	**k**	**pR^2**	**AIC**	**BIC**	**ΔAIC**	**ΔBIC**	***Rank***	**χ^2**	**P**	**R_S**	**p**	***Rank***
Null	−1		29366	29375	4007	3444						
$Geog_G$	9	0.061	27600	27683	2241	1753	3	158.60	p<0.0001	0.988	0.000	8
$Geog_{RS}$	6	0.061	27595	27650	2236	1720	2	132.84	p<0.0001	0.988	0.000	6
$Frag_G$	8	0.012	29020	29093	3661	3163	11	51.32	p<0.0001	0.794	0.006	11
$Frag_{RS}$	7	0.012	29018	29082	3659	3152	10	47.34	p<0.0001	0.818	0.004	9
$Land_G$	16	0.026	28637	28784	3278	2854	9	53.86	p<0.0001	0.903	0.000	10
$Land_{RS}$	12	0.026	28634	28745	3275	2815	8	47.41	p<0.0001	0.903	0.000	7
$Soil_G$	23	0.056	27763	27975	2404	2044	5	14.35	0.1104	0.976	0.000	2
$Soil_{RS}$	23	0.057	27745	27957	2386	2027	4	13.51	0.1409	0.988	0.000	1
$Clim_G$	21	0.054	27822	28015	2463	2085	7	80.75	p<0.0001	0.988	0.000	5
$Clim_{RS}$	18	0.054	27820	27986	2461	2055	6	69.58	p<0.0001	0.988	0.000	4
All Inclusive	62	0.141	25359	25930	0	0	1	31.87	0.0002	0.964	0.000	3

Note: $_G$ indicates the global model with no terms removed, $_{RS}$ indicates that the model was simplified using backwards elimination and IC scores. The 'All Inclusive' model includes all terms remaining from all isolated simplified models, with no further reductions.

Table 3.3. Estimated beta coefficients (β_i) and standard errors of environmental predictor variables included in Burrowing Owl home-range selection models. Values are indicated as part of each isolated reduced and simplified model and as part of the all-inclusive model. P values are shown to illustrate the relative change in significance of each term.

Class	Code	*Isolated Models (RS)*			*All-Inclusive Model*		
		Coef.	SE	P>z	Coef.	SE	P>z
Geography	East	-0.940	0.043	0.000	0.120	0.127	0.345
	$East^2$	0.078	0.005	0.000	-0.016	0.011	0.167
	North	-0.470	0.032	0.000	0.433	0.186	0.020
	$Elev^2$	-4.174	0.196	0.000	-5.098	0.744	0.000
	Slope	-0.291	0.018	0.000	-0.352	0.025	0.000
Grassland Fragmentation	gEdge	-0.135	0.011	0.000	-0.169	0.018	0.000
	gPatch	0.019	0.002	0.000	0.004	0.003	0.149
	gPatch_d	-0.385	0.101	0.000	0.144	0.112	0.199
	gSize	0.479	0.055	0.000	0.075	0.070	0.285
	$gSize^2$	-0.109	0.012	0.000	-0.039	0.014	0.005
	gRatio_10bp	-0.094	0.012	0.000	-0.023	0.015	0.126
Land-Use	dTVeg	1.352	0.139	0.000	-0.158	0.156	0.310
	$dTVeg^2$	-0.569	0.088	0.000	0.057	0.092	0.531
	dWater	-0.598	0.127	0.000	0.201	0.143	0.162
	dWet	-1.249	0.224	0.000	0.121	0.236	0.609
	$dWet^{0.5}$	1.308	0.309	0.000	0.188	0.340	0.579
	pGrass_25bp	2.538	0.178	0.000	6.309	0.453	0.000
	pHay_d	0.290	0.036	0.000	0.176	0.042	0.000
	pShrub	-6.370	0.847	0.000	0.552	0.941	0.558
	pTrees	-14.806	3.422	0.000	-7.984	3.753	0.033
	pWet	17.569	1.772	0.000	17.315	1.832	0.000
	$pWet^2$	-77.406	11.857	0.000	-75.404	11.750	0.000
Soil Characteristics	sCher	0.006	0.003	0.031	0.014	0.003	0.000
	$sCher^2$	-9.5E-05	2.7E-05	0.001	-1.5E-04	3.0E-05	0.000
	sGley	0.042	0.008	0.000	0.014	0.009	0.109
	$sGley^2$	-1.5E-03	4.3E-04	0.001	-9.5E-04	4.1E-04	0.022
	$sRego^2$	-3.2E-04	5.1E-05	0.000	-2.7E-04	5.5E-05	0.000
	sSolo_55bp	0.018	0.003	0.000	0.013	0.004	0.000
	sVert	0.018	0.003	0.000	0.029	0.004	0.000
	pmEoli	0.002	0.004	0.603	-0.004	0.004	0.293
	pmEoli_d	-0.304	0.094	0.001	-0.100	0.102	0.327
	pmFluv	-0.022	0.005	0.000	-0.011	0.005	0.043
	$pmFluv^{0.5}$	0.278	0.026	0.000	0.091	0.028	0.001
	pmLacu	-0.001	0.003	0.817	-0.005	0.003	0.104
	pmLacu_d	0.478	0.063	0.000	0.130	0.074	0.080
	pmTill	0.022	0.006	0.000	0.025	0.006	0.000
	$pmTill^2$	-7.8E-04	1.4E-04	0.000	-7.6E-04	1.5E-04	0.000
	$pmTill^3$	6.9E-06	9.7E-07	0.000	5.8E-06	1.0E-06	0.000
	sText_2	-0.324	0.144	0.024	-0.344	0.151	0.023
	sText_3	0.486	0.170	0.004	0.406	0.181	0.025
	sText_4	0.609	0.174	0.000	0.609	0.186	0.001
	sText_5	0.395	0.202	0.051	0.227	0.218	0.298
	sText_6	0.896	0.221	0.000	0.665	0.248	0.007

	sText_7	1.194	0.259	0.000	0.459	0.283	0.105
Climate	Ppt3	0.075	0.012	0.000	-0.013	0.013	0.331
	$Ppt3^2$	-2.7E-04	3.7E-05	0.000	3.1E-06	3.9E-05	0.937
	Tmin3	1.142	0.368	0.002	2.348	0.414	0.000
	$Tmin3^2$	0.012	0.004	0.001	0.021	0.004	0.000
	$Tmin3^3$	3.6E-05	1.2E-05	0.002	6.5E-05	1.3E-05	0.000
	Tmin4	0.376	0.072	0.000	-0.360	0.095	0.000
	$Tmin4^2$	0.006	0.002	0.000	-0.008	0.002	0.000
	Tmin5	0.592	0.077	0.000	-0.344	0.105	0.001
	$Tmin5^2$	-0.007	0.001	0.000	0.004	0.001	0.002
	Tmax3	0.056	0.015	0.000	0.020	0.021	0.327
	$Tmax3^2$	9.9E-04	5.3E-04	0.063	-2.4E-04	6.4E-04	0.706
	$Tmax3^3$	-3.9E-05	9.4E-06	0.000	-3.7E-05	1.1E-05	0.001
	Tmax4	11.973	1.962	0.000	8.032	2.130	0.000
	$Tmax4^2$	-0.102	0.017	0.000	-0.072	0.019	0.000
	$Tmax4^3$	2.9E-04	5.1E-05	0.000	2.2E-04	5.5E-05	0.000
	Tmax5	1.115	0.306	0.000	1.701	0.387	0.000
	$Tmax5^2$	-0.003	0.001	0.000	-0.005	0.001	0.000

Variable transformations are as indicated: superscript n = exponential to the power of n; _d = dichotomous variable included; _xbp = variable included a breakpoint value of x. Soil texture (sText) was a categorical variable coded in reference to category 1 (fine texture; course texture was 7).

Table 3.4. Model fit statistics determining whether or not interaction effects are present between vegetation management variables (continuous variables) and varying levels of large-scale soil/climate regimes (categorical variable; illustrated in Figure 3.3). Management variables were modelled with the soil/climate variable without interaction terms (w/ soil/climate) and with interaction terms (x soil/climate). A large change in AIC or BIC values (ΔAIC or ΔBIC >10) between models with and without interactions is highlighted in bold, italic font. * indicates variables with weak interaction effects, and ** indicates variables with strong interaction effects.

Variable	k	pR^2	AIC	BIC	ΔAIC	ΔBIC
pGrass **						
w/ soil/climate	4	0.062	27556	27593		
x soil/climate	6	0.064	27490	27545	***66***	***48***
pWet						
w/ soil/climate	4	0.062	27555	27592		
x soil/climate	6	0.062	27551	27607	4	-15
gEdge *						
w/ soil/climate	4	0.062	27547	27584		
x soil/climate	6	0.063	27525	27580	***22***	4
gSize **						
w/ soil/climate	4	0.062	27562	27599		
x soil/climate	6	0.063	27525	27580	***37***	***19***
gRatio						
w/ soil/climate	4	0.064	27489	27525		
x soil/climate	6	0.065	27482	27538	6	-12

Vegetation management variables: proportion of grassland (pGrass), proportion of wetland (pWet), grassland edge density (gEdge), grassland patch size (gSize), and grassland edge-to-area ratio (gRatio).

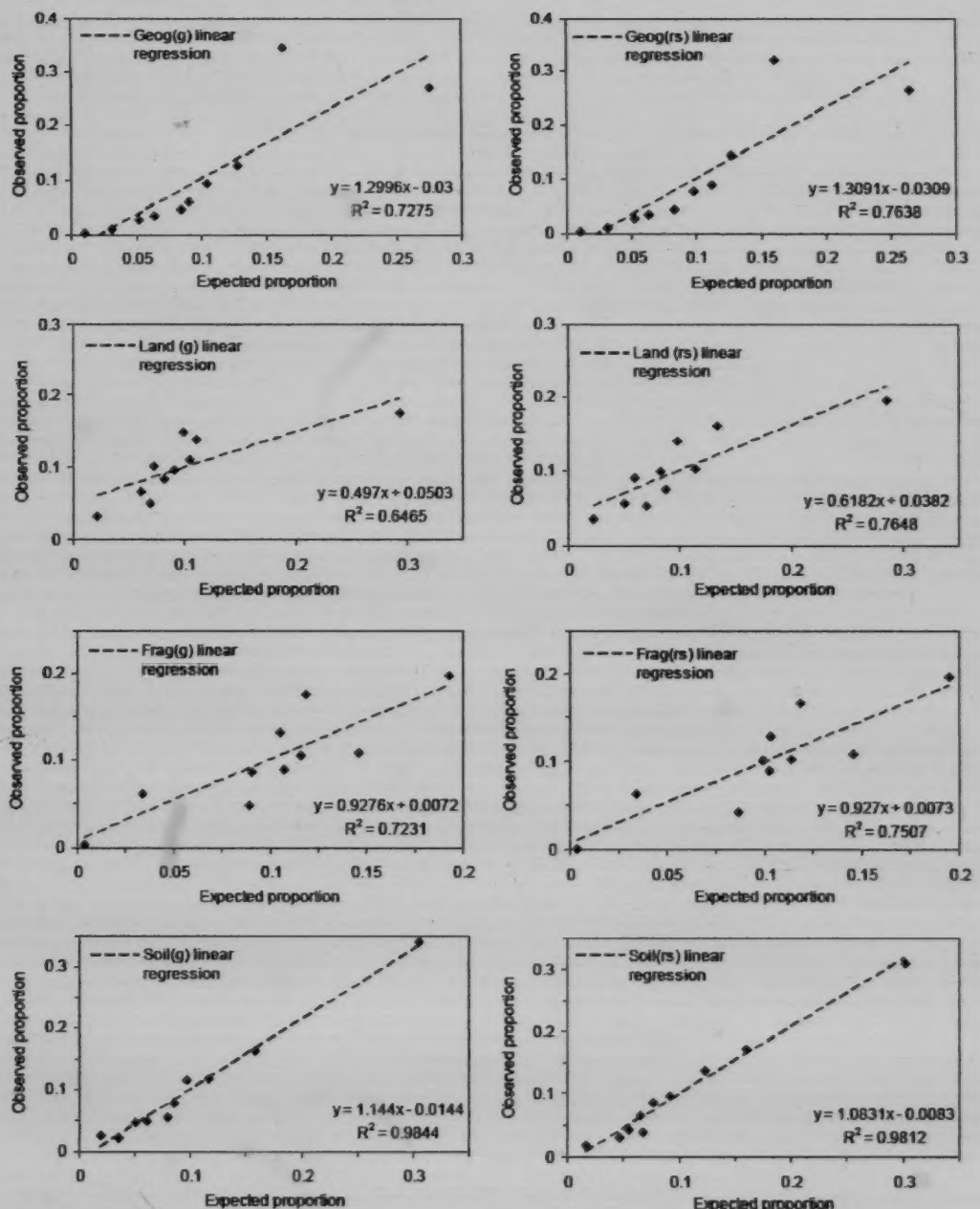

Figure 3.1. Expected versus observed proportion of evaluation data points for the temporally independent CWS data (n=558) for isolated candidate models (global, g, and simplified, rs) and the all-inclusive model. The fitted regression line is presented as a linear equation along with R^2 values.

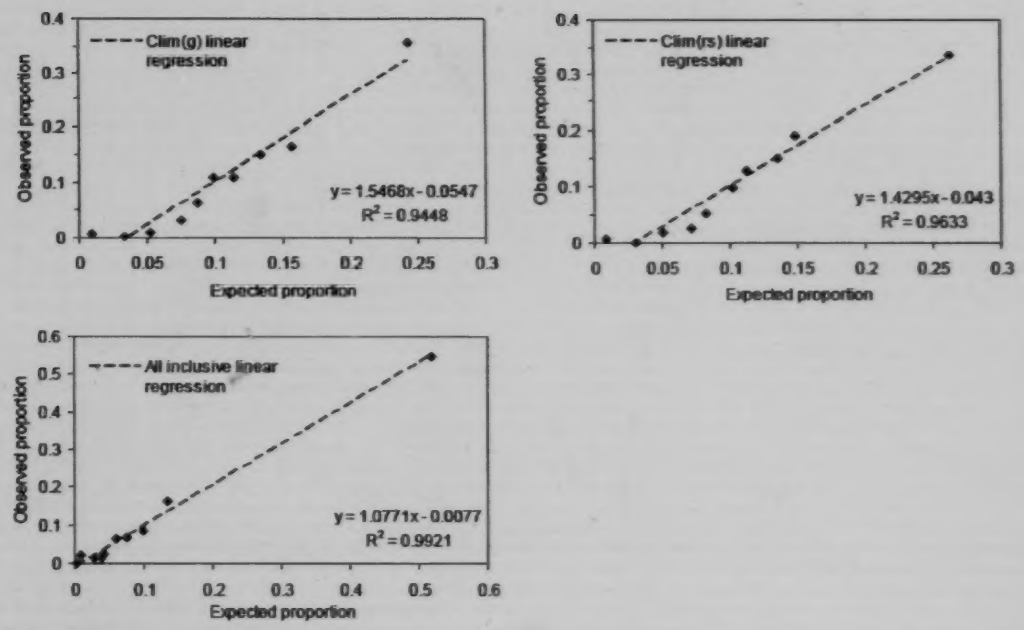

Figure 3.1. Continued.

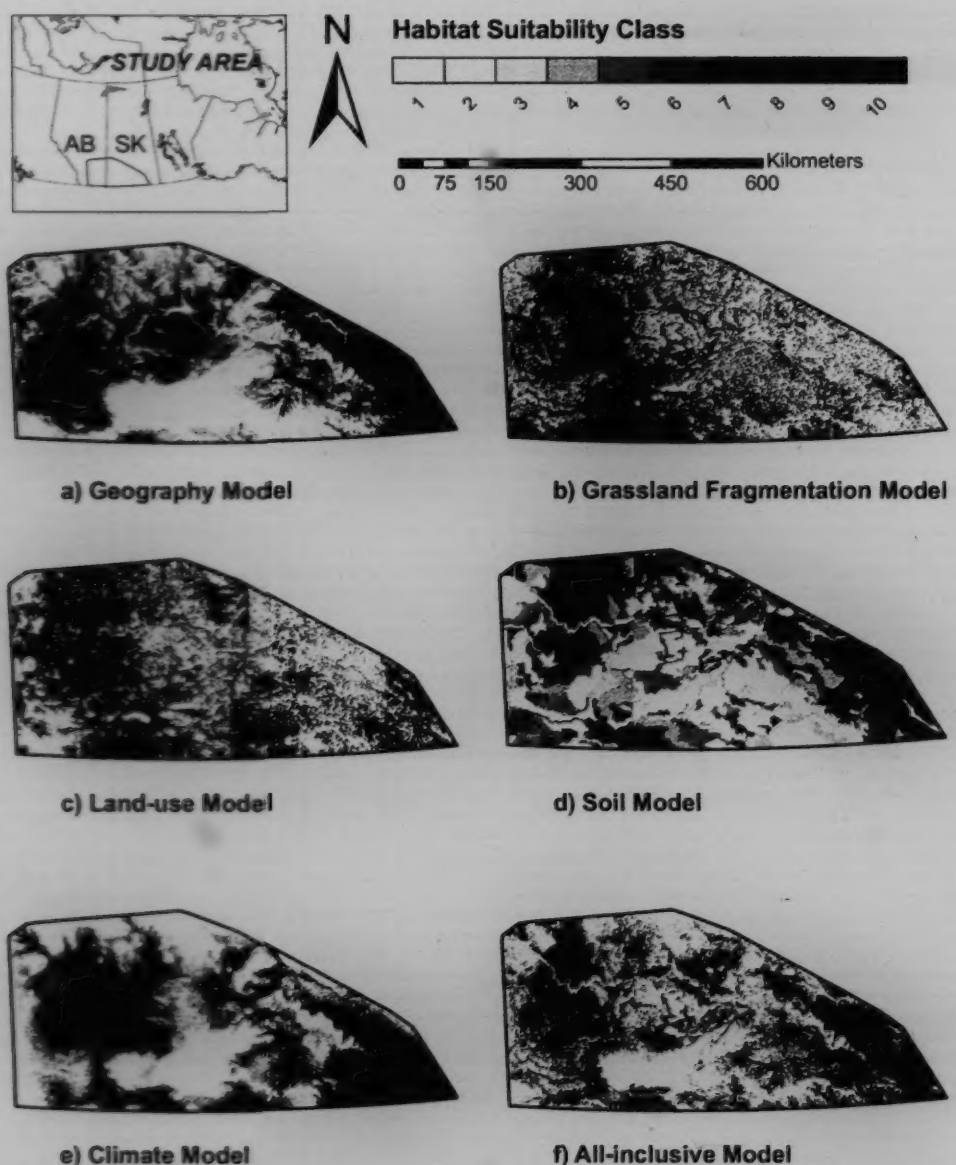

Figure 3.2. Relative indices of Burrowing Owl home-range selection in the grassland prairie region of Canada. These models were created using logistic regression resource selection functions (RSFs) and isolated variables sets (a-e) and all variable sets combined (f). Values range from low suitability class 1 (light) to highest suitability class 10 (dark green), where high suitability indicates where a Burrowing Owl is most likely to select its home-range.

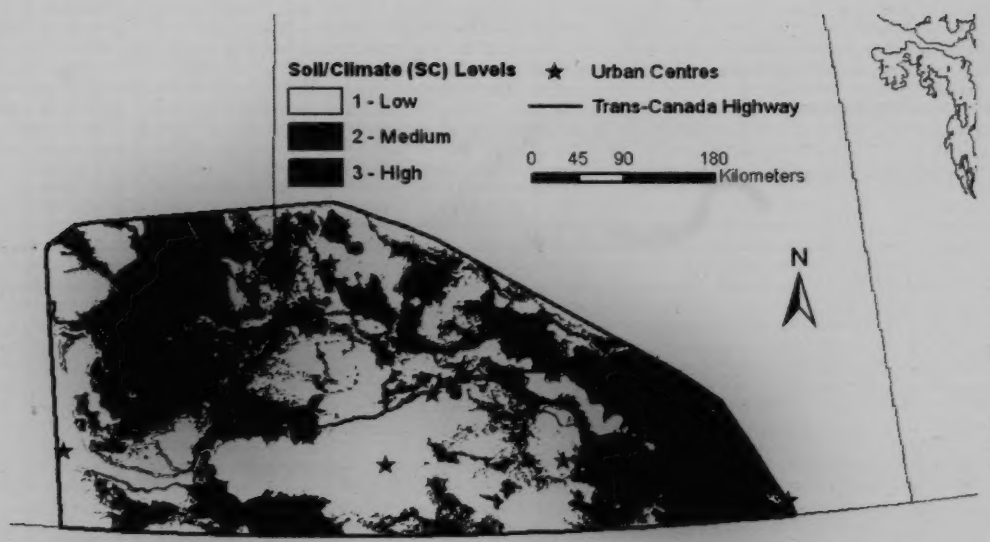

Figure 3.3. Soil/climate levels corresponding with relative probabilities of Burrowing Owl home-range selection within the study area. Soil/climate levels range from 1 to 3, where 1 = relatively low selection and 3 = high selection (as predicted by the simplified soil and climate models).

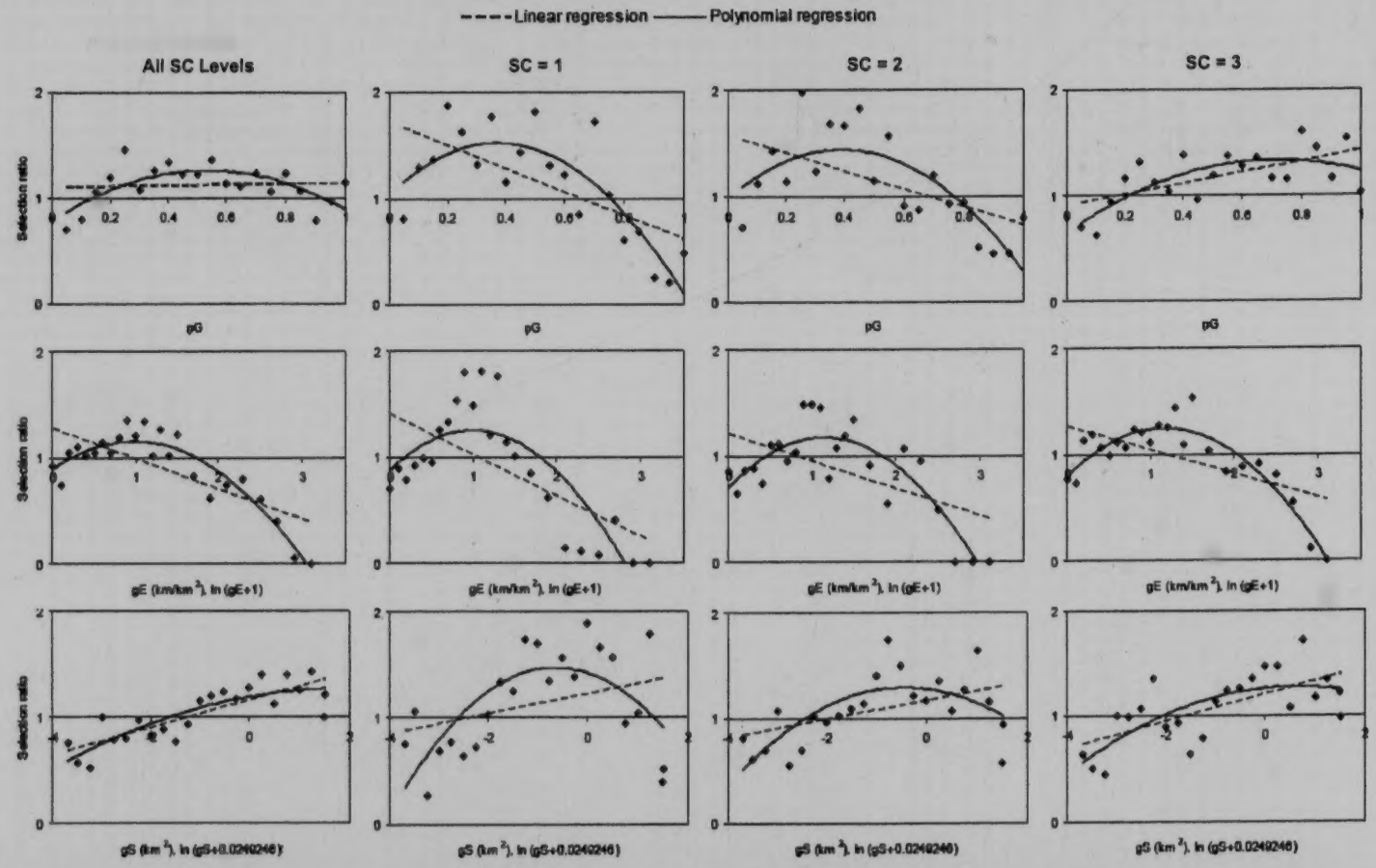

Figure 3.4. Burrowing Owl home-range selection ratios ($\hat{w}_i$) at varying levels of vegetation management reclassified into categories (proportion of grassland, pG; grassland edge density, gE; and grassland patch size, gS) within different Soil/Climate (SC) conditions. Selection ratios > 1 indicate selection for that category, while ratios < 1 indicate selection against. Ratios close to 1 (x-axis) indicate no selectivity. Linear and polynomial regression lines are provided as a visual aid for interpretation of selection ratio trends.

CHAPTER 4. IS BURROWING OWL HOME-RANGE SELECTION LINKED TO REPRODUCTIVE SUCCESS?

4.1 INTRODUCTION

Knowledge of how individuals select habitat is crucial in determining wildlife conservation strategies (Murphy and Noon, 1992; Engler et al. 2004; Norris, 2004; Johnson and Gillingham, 2005). However, determining disproportionate use of a habitat relative to its availability (Manly et al., 2002) may be insufficient to effectively characterize suitable and essential habitat for a species. Using habitat selection models alone as indicators of high-quality habitat assumes that animals make habitat selection decisions that are ideal for their fitness, and that this maximization of reproduction or survival leads to population increases in those selected areas (Fretwell and Lucas, 1970). However, occurrence- or abundance-based habitat selection does not always describe the optimum habitat composition or configuration for a species (Van Horne, 1983; Hobbs and Hanley, 1990). Therefore, before making any habitat management decisions based on habitat selection models, it is important to test whether or not habitat selection is related to a measure of habitat quality.

The exact nature of the relationship between habitat selection and habitat quality can lead to divergent management decisions. If there is either a positive or neutral relationship, habitat selection indices can be used to guide which suitable and essential habitats are in need of protection or management. In contrast, if habitat selection indices are negatively related to habitat quality, then high numbers of individuals are using areas that do not result in population growth (i.e., sinks; Pulliam, 1988; Delibes et al., 2001).

Population sinks can occur when dominant individuals take over prime breeding habitats, forcing a large number of sub-ordinates to crowd into marginal areas (Van Horne, 1983), or when an animal's ability to recognize and select high-quality habitat is impaired by anthropogenic disturbances (e.g., ecological traps; Bock and Jones 2004). If this negative relationship occurs, habitat selection indices should not be used to indicate high-priority habitats for species management (e.g. Remes 2003; Lloyd and Martin 2005; Weldon and Haddad 2005).

Discriminating between these alternative scenarios is crucial for threatened or endangered species recovery. In Canada, recovery teams must try to piece together as much information as possible to make effective recommendations for defining critical habitat. However, the rarity of individual animals, the desire to minimize human disturbance, and other logistic considerations often prevent adequate measurement of reproductive success for many endangered species. For example, Clark and Shutler (1999) reviewed the literature on a wide variety of avian species and found that only 29% of studies on endangered or threatened species were able to test for differences between successful and unsuccessful nesting habitat. Without an examination of habitat quality (in this case indicated by reproductive success), occurrence-based habitat selection models can result in recommendations for habitat protection that do little to help or may even hinder recovery of a population, despite the endangered species being present in relatively high densities.

To gain an understanding of the link between habitat use and habitat quality, it is important to consider large-scale factors that influence where a species can exist and also proximate factors that influence local reproductive success (e.g., nest survival and

number of fledglings produced). Habitat use and selection is often measured in terms of overall vegetation and other landscape qualities (e.g., soil, climate, geography) that are associated with potential resources for survival and reproduction that animals choose. However, reproductive success is often governed by dynamic fluctuations in the availability of resources, which at any given time may or may not correlate with overall vegetation and landscape characteristics that represent average resources. Simple models that relate overall reproductive success to habitat selection indices without accounting for other important proximate factors (e.g., temporal and weather dynamics) do not provide a thorough examination of how population persistence might be influenced by habitat use.

In Chapter 3, I created habitat selection models that predicted the distribution of Burrowing Owl home-ranges in the Canadian Prairies. In this chapter, my objective is to investigate if these habitat selection models and maps are useful tools for identifying high-quality habitat for Burrowing Owls. Specifically, I evaluate whether or not Burrowing Owl home-range selection is linked to reproductive success (i.e. nest survival and number of fledglings produced), accounting for proximate factors that influence productivity at a given point in time. I created nest-survival and fledgling production models that included the habitat selection indices generated in Chapter 3 as covariates, while accounting for breeding season temporal dynamics and short-term precipitation variables. High precipitation is one of the most common causes of nest failure and nestling mortality in Burrowing Owls (Wellicome 2000; Wellicome et al., unpubl. data) and needs to be considered when evaluating how large-scale selection covariates relate to reproductive success.

4.2 METHODS

4.2.1 Nest Monitoring Data

From 2003-2006, T. Wellicome from the Canadian Wildlife Service supervised a large-scale, multi-personnel project (hereafter 'CWS project') to assemble Burrowing Owl nest locations and associated reproductive information. The CWS project located nests throughout the study area by re-surveying known nesting sites and owl-occupied areas, and searching the surrounding landscape. Additional locations were obtained through cooperation with other biologists, land owners and managers with knowledge of breeding Burrowing Owl locations. Spatial coordinates of all monitored locations were recorded using Garmin GPS units.

Each year, the monitoring period began between 24 April (recoded to Day 1) and 2 May, and continued until the last nest was confirmed fledged or failed, between 30 July and 10 August. Therefore, the total monitoring period was standardized to 109 days (24 April to 10 August) for all years. Each location was visited approximately once/week during this monitoring period to confirm nesting stage, determine frequency and causes of nest failures, and quantify fledgling production. Because Burrowing Owls nest underground, most of this data was collected using home-made versions of Peeper™ Video Probe systems (Sandpiper Technologies, www.sandpipertech.com/video_inspection.html). The 'Peeper' system consists of a video-monitor headset, attached with a 4-meter fiber-optic cord to a video camera that has infrared sensors to view in total darkness (i.e., inside underground nest burrows). Nest chambers were monitored from the time of first detection until nest failure (destruction, depredation, flooding, or abandonment) or success could be determined.

Monitored locations were defined as nests based on evidence of reproduction: minimum of one egg or nestling in the burrow chamber, a brooding/incubating female, or two confirmed adults observed for at least one visit after the median egg laying date (May 9; Wellicome et al., unpubl. data).

Once a nest was confirmed, lay dates and hatch dates were estimated using methods described in Wellicome (2000) and a photo reference guide showing known-age nestlings (R. Poulin and D. Todd, unpubl. data). Visual observation of either the first egg or the first hatchling within the nest burrow provided the most accurate estimates; otherwise, back-dating from two or more mid-clutch counts was used, using the laying rate of 1 egg per 1.5 days (Wellicome, 2005). If nests were found after mid-clutch or after the first hatchling, young owlets were compared to the photo reference guide and older juveniles were aged using feather lengths when captured. If these estimates were unavailable for successful nests, the median egg laying date was used (n = 29). The monitoring start date for each nest was defined as the later of either the 1) first visit to the nest (i.e. when it was found) or 2) the estimated lay date (for a defined nest). Juvenile Burrowing Owls often wander and leave the nest for brief periods before permanent dispersal (Davies and Restani, 2006; T. Wellicome, pers. comm.). Therefore, a nest is considered successful (defining my metric of nest survival) if at least 1 juvenile survived to be 35-days old after hatching, which is the approximate start of the post-fledging period (Davies and Restani, 2006).

At successful nests, I estimated the maximum number of fledglings that reach 35 days by using four counting techniques between 25 and 35 days of age: 1) observations using high-powered spotting scopes and binoculars to view the nests from a distance on

multiple visits, 2) the last peeper count within the nest burrow, 3) trapping nestlings in the nest burrow entrance, and 4) remote video cameras that record the area around the nest entrance for 20 consecutive hours, including sunset and sunrise. In 2003, only the first two methods were used, so these nests were excluded from the fledgling production analysis. From 2004 to 2006, all four methods were implemented to acquire maximum fledgling counts (see Gorman et al. 2003 for a comparison of less-intensive methods; also, T. Wellicome, pers. comm.). The target video date for overnight camera recording was set at 30 days post-hatch +/- 5 days (T. Wellicome, pers. comm.), to account for potential missed fledglings that use satellite burrows when broods split between different burrows (typically after 30 days).

4.2.2 Model Covariates

Six habitat selection models were created in Chapter 3 that defined Burrowing Owl home-range distribution in the Canadian prairies. These models were based on categories of geography (elevation, slope and spatial gradients; Geog), grassland fragmentation (Frag), land-use (proportions and distances; Land), soil characteristics (texture, soil orders and parent material; Soil), climate (multi-year averages of temperatures and precipitation; Clim), and one model that included all categories (All-Inc). Habitat selection indices – equal-area bins ranging from 1 (low selection) to 10 (high selection) – were created from each of these models, and were compared in relation to nest success and fledgling production. Note that while habitat selection indices varied in predictive ability (see Chapter 3), all indices showed an increasing trend in the number of nests per equal-area bin, from low to high.

Weather was one of the principal causes of owl nest failure and individual nestling mortality (Wellicome 2000; Wellicome et al., unpubl. data). In particular, precipitation may affect reproduction through 1) nest flooding, 2) ability to hunt, and 3) prey activity or abundance. Because burrows are underground, nests are susceptible to flooding events under high amounts of precipitation. Burrowing Owls stay within nest burrows during high precipitation events (pers. observ.; T. Wellicome, pers. comm.), and this could lead to a loss of foraging time and, therefore, starvation of youngest nestlings (Wellicome, 2005) or abandonment of nesting attempts by adults. Lastly, high levels of precipitation are correlated with high mortality within broods, possibly due to a reduction in prey ability leading to starvation (Wellicome, 2000), reducing the number of fledglings produced per successful nest. Accordingly, four precipitation covariates were included in this analysis: PPT_max (maximum 1-day precipitation amount, mm), PPT_dur (binary variable indicating three or more sequential days of 7 mm or more of precipitation), PPT_mean (mean daily precipitation amount over nesting period), and PPT_7d (the number of days in which precipitation amounts equalled 7 mm or more). These variables were tested for both a linear trend and a quadratic functional form, as optimum precipitation amounts could exist that balance any positive effects of precipitation and negative effects of flooding, starvation and abandonment. These precipitation variables were created using the closest weather station to each nest, using data provided by the Meteorological Service of Canada, Prairie and Northern Region, Environment Canada.

Temporal variables included in the analysis were nest age, day in season, laying date/hatch day, and year. Nest age has the potential to affect nest survival rates because of differential predation risks caused by behavioural changes such as feeding and

visitation rates in altricial species (Dinsmore et al., 2002). The day in season (Date) could also affect nest survival as seasonal weather changes may occur, or predation risk may change later in the season when predator young are hungry and mobile. For similar reasons, laying date (represented by the 'age' of the nest at the start of the monitoring period; AgeDay1) and/or hatch day (Hatch) may affect both the nest survival and the number of fledglings produced. Year may be an important covariate for both nest survival and fledgling production analyses as weather patterns are dynamic from year to year, and there may be unmeasured gradients of predator and prey densities. Note that year was tested in all final models regardless of the univariate effect. Finally, interaction terms between precipitation, year, and habitat selection covariates were tested when appropriate.

4.2.3 Nest Survival

I used the nest survival module in Program MARK (White and Burnham, 1999; Dinsmore et al., 2002) to model the daily survival rates (DSR) of Burrowing Owl nests in relation to home-range habitat selection. Program MARK was first developed as free, easy to access statistical package for mark-recapture data. It currently hosts a number of options for modelling encounter-driven wildlife data, and allows for model evaluation using Akaike's Information Criterion (AIC) model selection techniques (Burnham and Anderson, 2002). The nest survival module uses a generalized linear modelling approach to model DSR using individual-, group- and time-specific covariates (Dinsmore et al., 2002; Rotella et al., 2004).

I performed two separate data analyses to maximize use of the data. The first analysis only included selection and temporal indices. I used a modified forward-

stepwise approach to build the models, using AIC corrected for small sample sizes (AIC_c; Burnham and Anderson, 2002) to rank the models at each step, and all models together. I first tested each individual covariate alone, and determined which variables explained more information than the constant (null; B0) model. I then combined those variables, and tested which combinations had the lowest AIC_c values. From this analysis, I was able to select the most appropriate temporal variables to include in the second analysis, and estimate if any of the habitat selection models had an effect on DSR.

For the second analysis, I included precipitation variables, habitat selection indices, and temporal variables that were found in the top-ranked models from the first analysis, using a similar model-building approach. Each of the precipitation variables were tested individually as linear and quadratic forms. The precipitation variable(s) that explained the most variation was then tested in combination with all six habitat selection indices to find the precipitation/selection model with the lowest AIC_c value. This model was then examined in various forms with temporal variables and potential interactions between precipitation and other variables, to determine the best models of DSR.

To evaluate the presence of a relationship between habitat selection models and DSR, I considered good evidence to be both 1) a strong positive/negative beta coefficient that was consistent among different model sets, and 2) a high model ranking with the inclusion of a habitat selection index. I also tested the predictive ability of the top-ranked nest survival model using a modified version of Johnson et al. (2006) K-fold cross validation evaluation methods for resource selection functions. I divided my dataset into 5 sets of data, of approximately equal sample size. I then withheld one (test) set, and used the remaining datasets to re-build the top ranked model, and then used that model to

predict DSR values for all data. These predicted values were then binned into 5 approximately equal-sized bins, ranked from lowest to highest DSR. From this point, I used the same methods described in Chapter 2 to compare the expected number of points per bin from the withheld dataset to the actual number of points in each bin using linear regression statistics (constant, β_0; slope, β_1; and R^2 value) and the χ^2 goodness-of-fit. I also included the Spearman rank correlation statistic (Boyce et al., 2002) as another measure of predictive performance, using a sample-size adjusted frequency compared to bin rank. This process was repeated for all K=5 sets of data, and averaged between all sets to evaluate predictive performance.

4.2.4 Fledgling Production

To evaluate fledgling production (number of owlets fledged) in relation to habitat selection indices, I used zero-truncated Poisson models. Total nest failure (number fledged = 0) was accounted for in the nest survival analysis and, therefore, excluded from this analysis. The response variable of number fledged was constrained between 1 and 10 (the maximum number of fledglings). The zero-truncated Poisson models were preferred to the zero-truncated binomial as there was not significant evidence of over dispersion ($G^2 = 0.00$, $p = 1.0$). I used a similar approach as with the nest survival data for analysis and model building. I performed two separate data analyses using AIC_c values to rank models and determine the best-fitting models. I performed all fledgling analyses in STATA 9.0 (STATA corp., 2005).

4.3 RESULTS

4.3.1 Nest Survival

A total of 623 potential Burrowing Owl nesting sites were located from 2003-2006. However, 143 sites had insufficient data for nest survival analysis; therefore, the sample size was reduced to 480 nests for the first analysis (without precipitation covariates). For this sample, apparent nest survival (proportion of successful nests) was 78%, while Mayfield nest survival (1-[(number of nest losses)/(total exposure days)]; Mayfield, 1961) was 72%. When precipitation covariates were included, sample size was further reduced to 369 nests, as 111 nests did not have sufficient weather data for the total monitoring period. For this sample size, apparent nest survival was 82%, and Mayfield nest survival was 76%.

For the first analysis, a quadratic function for nest age had the greatest single effect on daily survival rate, and the inclusion of nest initiation date (AgeDay1), year, land-use and soil habitat selection indices showed marginal improvements on the quadratic nest age model (Table 4.1; Δ AIC_c <8.3). When precipitation covariates were included in the second analysis, the top-ranked AIC_c model included the quadratic nest age term, a quadratic term for number of days with $\geq$ 7mm of precipitation (PPT_7d), year, the land-use habitat selection index, and an interaction between year and precipitation (PPT*Year; Table 4.2). However, the land-use index was not strongly related (beta coefficient = 0.071; confidence interval: -0.026 to 0.168).

Using K-fold cross validation (K=5) and a modified version of the Johnson et al. (2006) model evaluation methods, the top-ranked nest survival model was a weak predictor of nest survival for Burrowing Owls (mean R^2 = 0.58, mean R_s = 0.36; Table

4.3). However, linear regression statistics indicated that the model was proportional to the probability of survival (mean intercept (β_0) of 0, mean slope ~ 1) and the mean χ^2 test was non-significant. This indicates that the top-ranked model of nest survival fit the given data well, but did not have high predictive ability. Model-averaging was used to illustrate an overall best model using the three top-ranked nest survival models (Δ AIC_c <1, Table 4.4; Figure 4.1).

4.3.2 Fledgling Production

For the first fledgling analysis, 246 monitored Burrowing Owl nests survived to produce at least one offspring at 35 days, from 2004-2006. Of these nests, 52 nests had insufficient weather data for the total monitoring period, producing a sample size of 194 nests for the second analysis. The mean hatch day for all successful nests was approximately Day 44 of the monitoring period. Day 21 was the earliest hatch day, and Day 73 was the latest.

Hatch day had the single greatest effect on the number of fledglings produced, when precipitation covariates were not included in the analysis. None of the other single covariates tested explained more variation than the constant model (β_0; Table 4.5). When precipitation covariates were included in the analysis, the top ranked AIC_c model included hatch day and mean daily precipitation (PPT_mean; Table 4.6). The top three ranked models included the fragmentation habitat selection index, its interaction with mean precipitation (PPT*Frag), hatch day, and mean daily precipitation.

However, the top-ranked model had a pseudo-R^2 value of 0.032, the second model was 0.0327, and the third model was 0.033, indicating that none of these models fit the data well. Therefore, I used model-averaging to illustrate an overall best model for

fledgling production using the three top-ranked models (Δ AIC_c <3.4, Table 4.7; Figure 4.2).

4.4 DISCUSSION

Reproductive success of Burrowing Owls in Prairie Canada appears to be largely independent of home-range placement. The all-inclusive, soil, and climate selection indices were good predictors of Burrowing Owl use (see Chapter 3), yet none of the top models for nest survival or fledgling production included these indices as predictive variables. Instead, precipitation and temporal covariates were the most important factors. Bock and Jones (2004) found that, in most cases, high bird densities or high use of a particular habitat resulted in a greater recruitment *per capita* and per unit of land area. Though selection indices for both land-use and fragmentation were shown to have marginally positive influences on reproductive success, habitat selection indices were unrelated to reproductive success overall. Therefore, these results suggest that Burrowing Owl home-range habitat selection indices can be used as effective tools to help define areas for critical habitat. Each category of habitat selection described ~10% of the available landscape (almost 2 million hectares), with a greater number of nests (hence an increased owl density) in the highest categories. Because each category of selection did not differ with respect to reproductive success, the protection of habitats with the highest densities of owls should facilitate the highest overall productivity per unit area.

It is interesting that where Burrowing Owls selected home-range locations based on land-use and fragmentation attributes, they were more likely to experience slightly higher reproductive success. If land-use and grassland fragmentation were related to the historical population decline of Burrowing Owls in Canada (Haug et al., 1993;

Wellicome and Haug, 1995; COSEWIC 2006), perhaps these could be the most effective selection indices to guide conservation decisions. Simulated home-ranges in such areas are composed of at least 25% grassland with moderate patch sizes (e.g., not too small, but not encompassing the whole home-range), lower grassland edge densities but not below 10 units of edge-to-area, less shrubs and trees, and some wetland areas (see Chapter 3). Home-ranges that meet these criteria may provide three potential benefits to reproductive success. First, these attributes could describe areas with optimal prey availability and diversity, for instance meadow voles *(Microtus pennsylvanicus*) and sage brush voles (*Lemmiscus curtatus*), both of which are major components of the owl's diet (Poulin, 2003). Poulin (2003) related Burrowing Owl population fluctuations in south-central Saskatchewan to meadow vole population dynamics, and speculated that intensive cultivation for cereal farming may have negative impacts on vole irruptions. Grassland shows a strong negative correlation to cultivated land (Chapter 2 and 3), and meadow voles are related in the same manner (Poulin, 2003); therefore, the simulated home-range described above might provide optimum conditions for meadow vole populations. On the other hand, deer mice (*Peromyscus maniculatus*), another major component of the owl's diet are positively associated with cultivated land (Poulin, 2003). A second benefit of these optimum home-ranges may be a decreased predator presence, as areas with fewer shrubs and trees do not provide necessary nesting sites for most Burrowing Owl avian predators. Third, vegetation structure and landscape characteristics in these areas might mitigate the effects of high precipitation on Burrowing Owl productivity. For instance, grassland vegetation has different surface and root structure than cultivated vegetation, and these structures might ameliorate surface runoff and underground movement of

water, both of which lead to flooding of nest burrows. However, these hypotheses need to be tested to determine if any of these hypothesized benefits are actually conferred within the simulated home-range areas described above.

The highest probabilities of home-range habitat selection, dictated by soil and climate variables, were not important to nest survival or fledgling production. This may be due to the scale at which these variables were examined. Both indices predicted habitat selection at the home-range scale of the owl itself, and not necessarily the scales that are important to reproductive success, such as predation and weather events (Wellicome et al., 1997; Wellicome, 2000). Weather events, particularly precipitation, are mainly stochastic, and can occur on many different scales on the prairies, from localized rain showers, to regional snow storms. Conversely, predation risk can be modelled based on habitat; however, the scale depends on the predator, and not the owl. For instance, the home-range of the American badger (*Taxidea taxus*), a common predator of owls, ranges from 30 to 70 km^2 in British Columbia (Newhouse and Kinley, 2001). In South Dakota, Ferruginous Hawk *(Buteo regalis)* density was approximately 1 pair/17.4 km^2 (Lokemoen and Duebbert, 1976), which is equivalent to a radius of 2.35 km around a hawk nest. A multi-scale analysis incorporating ecologically-meaningful scales of potential predation events may show that habitat selection is actually correlated to reproductive success.

Precipitation covariates were found to be the most influential factors on reproductive success, followed by the temporal variables of nest age, hatch day, and year. However, by examining Figures 4.1 and 4.2, we see that an increase in number of days with 7mm or more of precipitation marginally increased nest survival, while lower mean

daily precipitation values produced a slightly higher number of fledglings. While this appears to be counter-intuitive, it is important to remember that nest survival and fledgling production are separate measures. Nest survival indicates the probability that a nest will successfully produce at least one offspring, while fledgling production is the actual number of fledglings produced by successful nests. Burrowing Owls forage at ephemeral and seasonal wetlands (Sissons, 2003), and an increase in single rain events (indicated by increased PPT_7d) may allow some wetland habitats to stay moist. The associated wetland vegetation may then be able to support increased prey populations for Burrowing Owls, allowing them to continue with a breeding attempt and keep at least one chick alive. On the other hand, prolonged rain over the entire nesting period (indicated by higher mean daily precipitation values) can decrease foraging opportunities for adult owls and force them to abandon their breeding attempt. Food availability is especially important during the nestling period (Wellicome, 2000), and therefore, if there is less foraging opportunity, the youngest chicks may be more vulnerable to starvation and death, which decreases the number of fledglings produced, even if the nesting attempt is not abandoned.

The importance of nest age and hatch day can be explained by behaviour and timing. In terms of nest age, daily survival rates decrease around the time of hatch, as activity around the nest increases (increased feeding rate; Poulin and Todd, 2006), which may allow for increased visual cues for predators. Once they pass the critical stage around hatching, daily survival rates begin to increase again. Possibly older, bigger chicks have a greater chance of survival, when they begin to feed themselves, learn to escape predators, and can sustain longer periods without food. Hatch days that occurred

earlier in the season produced a greater number of owl fledglings, similar to a study in South Dakota (Griebel and Savidge, 2007). This could be largely a reflection of avian predator dynamics. As the nestlings of predators hatch and grow later in the season, the adult predators need to hunt more often, and bring larger amounts of food back to the nest. Wellicome (2000) also showed a direct association between hatch date and fecundity, as Burrowing Owl clutch size was negatively correlated with estimated laying dates.

Regardless, the predictive ability for both nest survival and fledgling production models were quite low. Though I attempted to account for unmeasured gradients of predator populations and prey availability by including year as a covariate, this is not necessarily a suitable surrogate. The unpredictable nature of individual rain events may affect not only Burrowing Owl productivity, but also prey and predator population dynamics.

Future studies should quantify why certain habitats are used and selected by including direct measures of available resources (such as food) and limitations (predation risk), and also determine exactly what resources contribute to productivity and when this happens. For instance, foraging studies that define third-order habitat selection (Johnson, 1980) within the home-range should incorporate what resource items are being used and when they are being used optimally and link these directly to reproductive success. To further assess habitat quality, more demographic terms, such as adult survival and juvenile post-fledging survival, should be related to habitat characteristics.

4.5 CONCLUSION

The most predictive models of Burrowing Owl home-range habitat selection were not linked to nest survival or fledgling production. Instead, precipitation and temporal variables were the most important variables, and land-use and fragmentation habitat selection indices showed only a marginal effect. This indicates that it is sufficient for Burrowing Owl habitat protection and management efforts to focus on areas that are most likely to be selected for home-range use, as this selection neither increases nor decreases reproductive success. Alternatively, new models and maps can be created to predict nest survival and fledgling production using the original environmental predictor variables used to create the habitat selection indices. These maps could than be overlaid directly onto the habitat selection maps in order to delineate specific areas where high selection corresponds to high reproductive success (see similar work by Nielsen et al., 2006; Aldridge and Boyce, 2007). However, it is vital to look at foraging studies within breeding home-ranges, and also to incorporate measures of adult and juvenile survival within breeding grounds.

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Table 4.1. Summary of selection results for models of daily nest survival rate for Burrowing Owls in the Canadian Prairie region of Alberta and Saskatchewan, 2003-2006 (n = 480), excluding precipitation variables. The number of model parameters (k), Akaike's Information Criterion corrected for small sample sizes (AICc), ΔAICc (AICc model i – AICc minimum), Akaike weights, and model likelihood values are shown. Models were ranked based on ascending AICc values.

Model No.	Model Terms	k	AICc	Δ AICc	AICc Weights	Model Likelihood
NS19	{B0 + NestAge + NestAge^2 + AgeDay1 + Land + Soil + Year}	9	823.40	0.00	0.48	1.00
NS18	{B0 + NestAge + NestAge^2 + AgeDay1 + Land + Soil}	6	824.26	0.86	0.31	0.65
NS16	{B0 + NestAge + NestAge^2 + AgeDay1 + Land}	5	826.81	3.40	0.09	0.18
NS17	{B0 + NestAge + NestAge^2 + AgeDay1 + Soil}	5	827.83	4.42	0.05	0.11
NS13	{B0 + NestAge + NestAge^2 + AgeDay1}	4	828.58	5.18	0.04	0.08
NS14	{B0 + NestAge + NestAge^2 + Land}	4	830.25	6.85	0.02	0.03
NS15	{B0 + NestAge + NestAge^2 + Soil}	4	830.88	7.48	0.01	0.02
NS11	{B0 + NestAge + NestAge^2}	3	831.64	8.24	0.01	0.02
NS12	{B0 + AgeDay1}	2	850.36	26.95	0.00	0.00
NS05	{B0 + Land}	2	851.17	27.77	0.00	0.00
NS06	{B0 + Soil}	2	851.89	28.49	0.00	0.00
NS01	{B0}	1	852.91	29.50	0.00	0.00
NS08	{B0 + Year}	4	853.06	29.66	0.00	0.00
NS10	{B0 + NestAge}	2	853.94	30.53	0.00	0.00
NS07	{B0 + Clim}	2	854.31	30.91	0.00	0.00
NS04	{B0 + Frag}	2	854.52	31.11	0.00	0.00
NS03	{B0 + Geog}	2	854.67	31.27	0.00	0.00
NS02	{B0 + All-Inc}	2	854.84	31.43	0.00	0.00
NS09	{B0 + Date}	2	854.90	31.49	0.00	0.00

Table 4.2. Summary of selection results for models of daily nest survival rate for Burrowing Owls in the Canadian Prairie region of Alberta and Saskatchewan, 2003-2006 (n=369), accounting for precipitation conditions. The number of model parameters (k), Akaike's Information Criterion corrected for small sample sizes (AICc), ΔAICc (AICc model i – AICc minimum), Akaike weights, and model likelihood values are shown. Models were ranked based on ascending AICc values.

Model No.	Model Terms	k	AICc	Δ AICc	AICc Weights	Model Likelihood
NSP21	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year + Land + PPT*Year}	15	497.42	0.00	0.32	1.00
NSP24	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year + PPT*Year}	14	497.42	0.00	0.32	1.00
NSP23	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year + Land + PPT*Year + PPT*Land}	17	497.94	0.52	0.25	0.77
NSP19	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year + Land}	9	501.90	4.49	0.03	0.11
NSP18	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year}	8	502.09	4.67	0.03	0.10
NSP22	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year + Land + PPT*Land}	11	502.78	5.37	0.02	0.07
NSP20	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Year + AgeDay1}	9	503.60	6.18	0.01	0.05
NSP16	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + Land}	6	525.94	28.53	0.00	0.00
NSP17	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2 + AgeDay1}	6	528.45	31.04	0.00	0.00
NSP15	{B0 + NestAge + NestAge^2 + PPT_7d + PPT_7d^2}	5	528.89	31.48	0.00	0.00
NSP12	{B0 + PPT_7d + PPT_7d^2 + Land}	4	534.24	36.83	0.00	0.00
NSP08	{B0 + PPT_7d + PPT_7d^2}	3	537.28	39.86	0.00	0.00
NSP05	{B0 + PPT_7d}	2	538.12	40.70	0.00	0.00
NSP10	{B0 + PPT_7d + PPT_7d^2 + Geog}	4	538.36	40.94	0.00	0.00
NSP09	{B0 + PPT_7d + PPT_7d^2 + All-Inc}	4	539.10	41.69	0.00	0.00
NSP13	{B0 + PPT_7d + PPT_7d^2 + Soil}	4	539.23	41.82	0.00	0.00
NSP11	{B0 + PPT_7d + PPT_7d^2 + Frag}	4	539.24	41.83	0.00	0.00
NSP14	{B0 + PPT_7d + PPT_7d^2 + Clim}	4	539.27	41.85	0.00	0.00
NSP07	{B0 + PPT_mean + PPT_mean^2}	3	550.58	53.17	0.00	0.00
NSP06	{B0 + PPT_max + PPT_max^2}	3	553.38	55.96	0.00	0.00
NSP02	{B0 + PPT_max}	2	569.96	72.55	0.00	0.00
NSP01	{B0}	1	575.46	78.04	0.00	0.00
NSP04	{B0 + PPT_mean}	2	576.97	79.56	0.00	0.00
NSP03	{B0 + PPT_dur}	2	576.99	79.57	0.00	0.00

Table 4.3. K-fold cross validation results of top-ranked nest survival model, NSP21, for Burrowing Owls in the Canadian Prairies, 2003-2006 (Table 4.2). Evaluation was performed using a modified version of Johnson et al. (2006) methods for evaluating Resource Selection Functions with linear regression and goodness-of-fit statistics (χ^2), and sample-size adjusted Spearman rank correlation statistics (Rs).

	Linear Regression			*Goodness-of-Fit*		*Spearman*	
Test Bin	β_0	**B1**	R^2	χ^2	**p**	**Rs**	**p**
K=1	-0.05	1.26	0.86	0.00	0.95	0.20	0.75
K=2	-0.02	1.10	0.87	0.00	0.98	0.70	0.19
K=3	-0.09	1.47	0.56	0.00	0.89	0.10	0.87
K=4	0.22	-0.08	0.00	3.12	0.54	0.20	0.75
K=5	-0.03	1.17	0.63	0.00	0.70	0.60	0.28
Mean	0.00	0.99	0.58	0.62	0.81	0.36	0.57

Table 4.4. Beta coefficient estimates and standard errors (SE) for the top three AICc ranked models (NSP21, NSP24, NSP23) of nest survival for Burrowing Owls in the Canadian Prairies, 2003-2006. Model averaging results are presented as beta coefficients for the unweighted average and the final weighted average model.

	NSP21		NSP24		NSP23		*Unweighted Average*	*Weighted Average*
Term	**Coef.**	**SE**	**Coef.**	**SE**	**Coef.**	**SE**		
B0	7.360	1.496	8.011	1.428	9.233	1.883	8.202	8.116
NestAge	-0.185	0.045	-0.186	0.045	-0.185	0.045	-0.185	-0.185
$NestAge^2$	0.002	0.001	0.002	0.001	0.002	0.001	0.002	0.002
PPT_7d	0.355	0.601	0.308	0.596	-0.470	0.763	0.065	0.109
PPT_7d^2	-0.019	0.064	-0.015	0.063	0.046	0.078	0.004	0.0004
2004	-0.659	1.446	-0.846	1.438	-1.009	1.429	-0.838	-0.823
2005	-3.343	1.338	-3.565	1.326	-3.637	1.329	-3.515	-3.505
2006	-4.683	1.417	-4.850	1.414	-4.982	1.424	-4.838	-4.826
Land	0.071	0.050	0.000	---	-0.161	0.143	0.009	0.023
7d*2004	0.059	0.676	0.116	0.669	0.217	0.673	0.208	0.207
7d*2005	0.282	0.637	0.349	0.631	0.407	0.639	0.618	0.635
7d*2006	1.140	0.661	1.165	0.658	1.282	0.668	0.805	0.766
$7d^2$*2004	-0.002	0.070	-0.008	0.068	-0.016	0.071	-0.007	-0.006
$7d^2$*2005	0.003	0.067	-0.002	0.066	-0.008	0.068	-0.023	-0.024
$7d^2$*2006	-0.061	0.069	-0.063	0.068	-0.073	0.070	-0.045	-0.042
7d*Land	0.000	---	0.000	---	0.102	0.057	0.034	0.028
$7d^2$*Land	0.000	---	0.000	---	-0.008	0.005	-0.003	-0.002
AICc Weight	0.32		0.32		0.25			

Table 4.5. Summary of selection results for zero-truncated Poisson models of fledgling production for Burrowing Owls in the Canadian Prairie region of Alberta and Saskatchewan, 2004-2006 (n=246), excluding precipitation variables. The number of model parameters (k), Akaike's Information Criterion corrected for small sample sizes (AICc), ΔAICc (AICc model i – AICc minimum), Akaike weights, and model likelihood values are shown. Models were ranked based on ascending AICc values.

Model No.	Model Terms	k	AICc	Δ AICc	AICc Weights	Model Likelihood
FP09	{B0 + Hatch}	2	1013.75	0.00	1.00	1.00
FP01	{B0}	1	1032.85	19.10	0.00	0.00
FP07	{B0 + Clim}	2	1033.40	19.66	0.00	0.00
FP04	{B0 + Frag}	2	1033.64	19.89	0.00	0.00
FP05	{B0 + Land}	2	1034.16	20.42	0.00	0.00
FP03	{B0 + Geog}	2	1034.27	20.52	0.00	0.00
FP06	{B0 + Soil}	2	1034.42	20.68	0.00	0.00
FP02	{B0 + All-Inc}	2	1034.53	20.79	0.00	0.00
FP08	{B0 + Year}	3	1036.65	22.90	0.00	0.00

Table 4.6. Summary of selection results for zero-truncated Poisson models of fledgling production for Burrowing Owls in the Canadian Prairie region of Alberta and Saskatchewan, 2004-2006 (n=194), accounting for precipitation. The number of model parameters (k), Akaike's Information Criterion corrected for small sample sizes (AICc), ΔAICc (AICc model i – AICc minimum), Akaike weights, and model likelihood values are shown. Models were ranked based on ascending AICc values.

Model No.	Model Terms	k	AICc	Δ AICc	AICc Weights	Model Likelihood
FPP15	{B0 + Hatch + PPT_mean}	3	800.65	0.00	0.60	1.00
FPP16	{B0 + Hatch + PPT_mean + Frag}	4	802.17	1.52	0.28	0.47
FPP17	{B0 + Hatch + PPT_mean + Frag + PPT*Frag}	5	804.05	3.39	0.11	0.18
FPP11	{B0 + PPT_mean + Frag}	3	814.47	13.82	0.00	0.00
FPP04	{B0 + PPT_mean}	2	815.08	14.43	0.00	0.00
FPP09	{B0 + PPT_mean + All-Inc}	3	816.05	15.40	0.00	0.00
FPP12	{B0 + PPT_mean + Land}	3	816.20	15.55	0.00	0.00
FPP13	{B0 + PPT_mean + Soil}	3	816.34	15.69	0.00	0.00
FPP10	{B0 + PPT_mean + Geog}	3	816.67	16.02	0.00	0.00
FPP07	{B0 + PPT_mean + PPT_mean^2}	3	817.04	16.39	0.00	0.00
FPP14	{B0 + PPT_mean + Clim}	3	817.10	16.45	0.00	0.00
FPP05	{B0 + PPT_7d}	2	820.20	19.55	0.00	0.00
FPP08	{B0 + PPT_7d + PPT_7d^2}	3	820.90	20.25	0.00	0.00
FPP02	{B0 + PPT_max}	2	820.96	20.31	0.00	0.00
FPP06	{B0 + PPT_max + PPT_max^2}	3	821.43	20.78	0.00	0.00
FPP01	{B0}	1	822.78	22.13	0.00	0.00
FPP03	{B0 + PPT_dur}	2	824.78	24.13	0.00	0.00

Table 4.7. Beta coefficient estimates and standard errors (SE) for the top three AICc ranked models (FPP15, FPP16, FPP17) of fledgling production for Burrowing Owls in the Canadian Prairies, 2004-2006, from Table 4.4. Model averaging results for beta coefficients are presented as the unweighted average and the final weighted average model.

	FPP 15		FPP16		FPP17		Unweighted Average	Weighted Average
Term	Coef.	SE	Coef.	SE	Coef.	SE		
B0	2.674	0.209	2.582	0.243	2.397	0.453	2.551	2.618
Hatch	-0.016	0.004	-0.016	0.004	-0.015	0.004	-0.016	-0.016
PPT_mean	-0.145	0.047	-0.147	0.047	-0.078	0.149	-0.124	-0.138
Frag	0.000	---	0.010	0.013	0.034	0.053	0.015	0.007
mean*Frag	0.000	---	0.000	---	-0.009	0.020	-0.003	-0.001
AICc Weight	0.60		0.28		0.11			

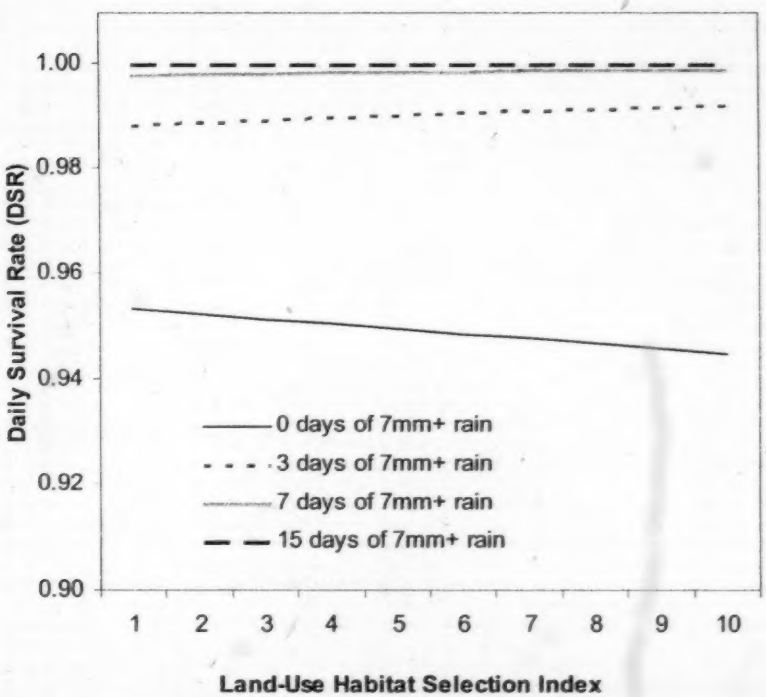

Figure 4.1. Estimated relationship between the land-use habitat selection index (created in Chapter 3) on daily survival rate (DSR) for Burrowing Owls in the Canadian prairies, 2003-2006, when accounting for the effects of precipitation (number of days with 7mm or more of rain). Estimates are taken from the model weighted average of the top 3 AICc ranked models, shown in Table 4.6. Nest age was held constant at 30 days (approximate day in nesting period when the first egg hatches).

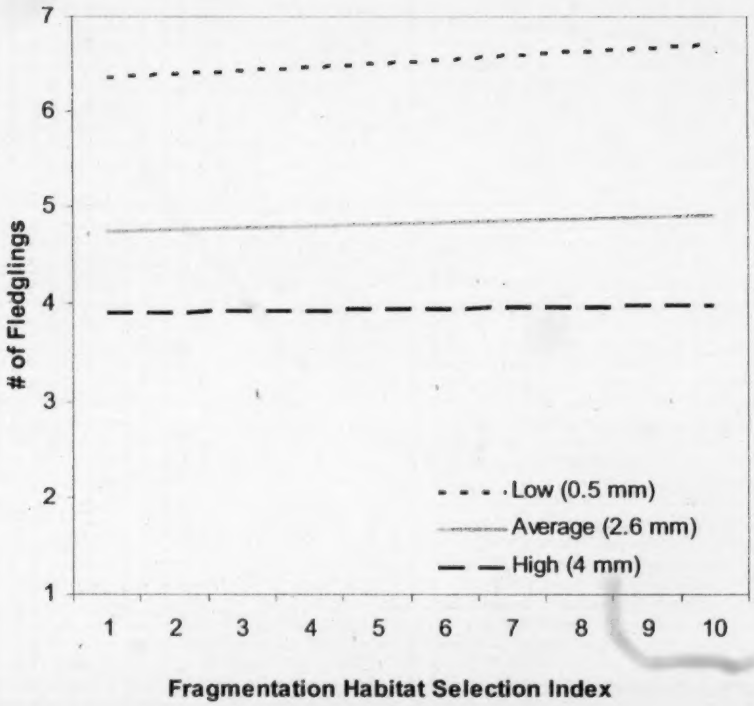

Figure 4.2. Estimated relationship between the fragmentation habitat selection index (created in Chapter 3) on fledgling production (number of fledglings produced per successful nest) for Burrowing Owls in the Canadian prairies, 2004-2006, when accounting for mean daily precipitation over the nesting period. Estimates are taken from the model weighted average of the top 3 AICc ranked models, shown in Table 4.7. Hatch day was held constant at Day 44 of monitoring period (mean hatch day over 3-year period where Day 1 = April 24).

CHAPTER 5. GENERAL CONCLUSIONS: SYNTHESIS AND RECOMMENDATIONS

5.1 RESEARCH SUMMARY

The purpose of this thesis was to investigate several technical and ecological aspects of defining potential critical habitat, based on home-range habitat selection by Burrowing Owls in the Canadian Prairies. Specifically, I compared two different species distribution modelling techniques, an Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002) and a logistic regression Resource Selection Function (RSF; Manly et al., 2002). My comparison revealed that ENFA models can provide robust ecological indications of habitat suitability, while a carefully designed RSF model can provide better spatially explicit predictions. I then created six different RSFs describing home-range habitat selection, and determined that large-scale, abiotic factors of soil and climate can accurately predict Burrowing Owl home-range selection. These factors create unique habitat conditions that are independent of the vegetative characteristics of land-use. Finally, I examined the link between high-use areas and reproductive success, using the home-range habitat selection models as potential covariates. There was no relationship between home-range habitat selection and measures of reproductive success. Overall, my study provides one of the first spatially explicit descriptions of potential critical habitat for the Burrowing Owl recovery team.

5.2 LIMITATIONS AND RECOMMENDED RESEARCH

My research fills an important knowledge gap required for identifying critical habitat for Burrowing Owls in Canada by evaluating home-range selection patterns and their relationships to reproductive success. However, this research was designed only to narrow the potential areas within which critical habitat should be designated, which is one of the first steps in the process. As well, there are some limitations to my study that need to be addressed, the first being the quality of the location dataset used to create all of my habitat selection models.

To gather as much information as possible from such a large study area, I used a haphazard collection of Burrowing Owl location data that included data from biologists, landowners, oil and gas companies, and incidental observations from the general public. In an ideal scientific analysis, species presence data is gathered through systematic surveys conducted by trained biologists throughout the landscape to provide objective, unbiased sampling. However, because these data were collected without a specified random or stratified sampling scheme, biases may be present in the data that might influence conclusions that are drawn. For instance, Burrowing Owls are most likely to be observed by humans in areas that are frequented by humans. This may lead to a greater number of owls known to associate with human land-use, creating a positive habitat selection coefficient. Though I did include anthropogenic habitats, such as hayed land, I did not include many anthropogenic features, such as roads, buildings, and pipelines, in my analysis of home-range habitat selection. This means that I avoided any spurious associations with these features; however, I was also unable to account for their potential influences. In addition, an increase in the number of observers in certain areas leads to an increase in sample size, and potentially multiple counts of individual owls. I removed

extra counts of owls by screening my dataset before model building, removing multiple counts by different observers in the same year within the same area (i.e., a quarter-section). On the other hand, this also introduces an error of omission, as I may have deleted counts that were actually separate within the same quarter-section. Ideally, systematic surveys would be performed across the entire study region. The model I provide should be used in any survey design for the owls, and could be used to stratify sampling effort to minimize costs of future sampling.

When attempting to link habitat use to habitat quality, I related home-range selection patterns to only nest survival and fledgling production. These reproductive measures were a good starting point for a study of habitat quality in Burrowing Owls because the population on the Regina Plain was found to be most sensitive to the production of young as opposed to mortality at older adult stages (Franken and Wellicome, 2003). However, my study indicates the Burrowing Owl reproductive success within the Canadian Prairies is quite high (75-85% apparent nest success, with an average of 4.7 fledglings per successful nest; see Chapter 4). Therefore, other important demographic terms that were not measured in my study may be closely related to variations in environmental variables and affect population persistence and growth; specifically, adult or juvenile survival in breeding, wintering, or migration areas. I believe one of the most pressing knowledge gaps at the moment is research into the migratory patterns and survival mechanisms of the Canadian population of Burrowing Owls.

I also emphasize that my results only provide insight into second-order selection patterns (Johnson, 1980). Though this was an area that was severely lacking in the

published literature, future studies also need to increase our understanding of third- and fourth-order selection processes. In particular, foraging studies within home-ranges should be useful for pinpointing a more definitive range of useful habitat characteristics, and how Burrowing Owls use resources when their availabilities differ under a variety of abiotic regimes. This future research may be facilitated by the current trend in avian habitat selection studies incorporating multi-scale or hierarchal selection patterns within one model (Kristan and Scott, 2006), and should be attempted for Burrowing Owls.

5.3 MANAGEMENT IMPLICATIONS

Effective critical habitat designations require: 1) quantitative methods capable of creating spatially-explicit predictions; 2) recognition of spatial and temporal scale when making decisions about what habitat is critical; and 3) ecologically based criteria of habitat needs that are linked to the main demographic factors that limit population growth in individual species. My study provides the first steps in this process, and fills this knowledge gap for Burrowing Owls in terms of second-order (Johnson, 1980) home-range selection patterns. I also provide a spatially-explicit outline of potential areas within which critical habitat designations can include maximum productivity by the population per unit area. The recovery team can use these results to stratify future Burrowing Owl surveys and to make decisions on prioritizing habitat conservation among regions, as well as potential areas for future research on third- and fourth-order selection.

These models are necessarily limited by currently available data, so to examine finer scales of selection, recovery teams need to address the need for more detailed and spatially-accurate data. In chapter 3, I pointed out potential mechanisms that allow for some areas to be used more than their availability; however, these processes cannot be

examined in detail until we have the fine-scale data to address them. For instance, we may need to distinguish certain grass-species communities (e.g., pastures with native vs. introduced grass species) to determine which provide more available prey. As well, the pixel size of most of my datasets (30-m) may have played a role in the final inferences for my statistical comparison in chapter 2. Perhaps a smaller pixel size (5-10 m) will help differentiate important relationships from spurious ones. I recommend that all recovery teams and governments that are working in the same study region combine resources to create and provide accurate, detailed, and up-to-date spatial data within the grassland ecosystem.

Finally, my results provide indications of large areas of potential critical habitat, but we still do not know how much of this land need be protected to ensure survival and recovery of the Burrowing Owl population. I examined two demographic measures, nest survival and fledgling production; however, a detailed population viability analysis should be combined with habitat selection models to provide a population estimate and growth rate. Aldridge and Boyce (2007) provide an example of such habitat population viability analysis using Resource Selection Functions, and I recommend that recovery teams use this as an approach to establish minimum land requirements.

5.4 LITERATURE CITED

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